

## Review

# Metabolic Pathways in Plants Under Arsenic Stress: Mechanisms, Responses, and Mitigation Strategies

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## Highlights

### What are the main findings?

- Arsenic disrupts primary and secondary metabolism in plants. Phosphate transport, water regulation, and nutrient balance are altered.
- Rhizosphere microbiota modulate arsenic toxicity and plant performance.

### What are the implications of the main findings?

- Multi-omics and crop breeding accelerate the development of arsenic-tolerant crops.

## Abstract

Arsenic (As) is a highly toxic metalloid that can be absorbed by plants, inducing stress that disrupts vital physiological processes. In response, plants activate defense mechanisms that allow them to cope with As-induced stress. This review provides a comprehensive overview of the metabolic pathways involved in plant responses to As stress, focusing on the mechanisms of As uptake and transport, metabolic and antioxidant responses, molecular regulation, and mitigation strategies that contribute to plant adaptation and tolerance. As exposure disrupts primary metabolism by impairing photosynthesis, the Calvin cycle, and carbon and energy metabolism, while also altering aquaporin-mediated transport and phosphate homeostasis. In addition, As induces oxidative stress, leading to increased lipid peroxidation and enhanced activities of antioxidant enzymes, including superoxide dismutase (SOD), ascorbate peroxidase (APX), and glutathione reductase (GR). It also affects secondary metabolism by modifying the biosynthesis and accumulation of specialized metabolites involved in stress tolerance. Overall, the evidence reviewed indicates that As can induce changes in both primary and secondary metabolic pathways. Although primary metabolic alterations are relatively well documented, information regarding changes in secondary metabolites, including phenolics and flavonoids, remains limited. Therefore, future research should integrate genomics, transcriptomics, proteomics, and metabolomics to elucidate the molecular basis of As tolerance and support modern crop breeding programs aimed at developing arsenic-tolerant cultivars. Moreover, this knowledge is fundamental for mitigating the impact of As on major food crops such as rice, wheat, maize, and vegetables, where arsenic contamination can reduce productivity,



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compromise crop quality, and increase the risk of As entry into the food chain. Furthermore, the mechanistic insights gained from these crops may serve as a basis for developing mitigation strategies applicable to other agriculturally important species.

**Keywords:** arsenic; detoxification; plant stress; primary metabolites; secondary metabolites

## 1. Introduction

Arsenic (As) is a highly toxic metalloid that occurs naturally in the Earth's crust and is mobilized by both natural and anthropogenic activities [1–3]. This metalloid is found in minerals such as arsenopyrite ( $\text{FeAsS}$ ), realgar ( $\text{As}_4\text{S}_4$ ), and orpiment ( $\text{As}_2\text{S}_3$ ), among others [4,5]. Weathering and decomposition of these minerals release considerable amounts of As into soil and water [6]. In addition, industrial activities such as mining and metal refining release large amounts of As into the environment [7,8]. In the environment, As occurs in various chemical forms, both organic and inorganic. These forms are mobilized within the water–soil–plant system, thus posing a threat to human health [9,10] and the environment. As occurs mainly in the (III) and (V) oxidation states, both of which are extremely toxic and hazardous. These chemical forms differ in their mobility, bioavailability, and uptake mechanisms in plants, thereby influencing arsenic accumulation and phytotoxicity [11,12].

In its organic forms, As occurs mainly as monomethylarsonic acid (MMA) and dimethylarsinic acid (DMA) [13,14]. Both organic species also pose a considerable toxicological risk to human health. Once present in irrigation water, As can be taken up by plants to different extents, depending on their sensitivity [3,5]. In general, As uptake creates stressful and toxic conditions for plant growth [15]. It also induces oxidative stress that affects key developmental processes such as protein synthesis, photosynthesis, and cellular respiration [16,17]. In aqueous solution at physiologically relevant pH, As(V) exists predominantly as the dihydrogen arsenate ( $\text{H}_2\text{AsO}_4^-$ ) and hydrogen arsenate ( $\text{HAsO}_4^{2-}$ ) anions, which are chemically analogous to the phosphate species dihydrogen phosphate ( $\text{H}_2\text{PO}_4^-$ ) and hydrogen phosphate ( $\text{HPO}_4^{2-}$ ), respectively. This structural similarity confers a high affinity for phosphate transporters, particularly Pht1;1 and Pht1;4 [18]. When plants take up As(V), it competes with  $\text{PO}_4^{3-}$ , severely affecting ATP production and plant growth [8,13,19]. On the other hand, As(III) can be absorbed through aquaporin channels, where it binds to the sulfhydryl groups of proteins, damaging cell membranes and ultimately leading to cell death [20,21]. Finally, As exposure induces the overproduction of reactive oxygen species (ROS), leading to oxidative stress [20,21]. In response, plants activate their antioxidant defense system, increasing the activity and/or expression of enzymes such as superoxide dismutase (SOD), ascorbate peroxidase (APX), glutathione reductase (GR), as well as the content of non-enzymatic antioxidants such as glutathione (GSH), all of which participate in ROS detoxification [22]. Plants that adapt to stress conditions activate a series of defense mechanisms, such as antioxidant enzyme production, osmolyte accumulation, phytochelatin synthesis, and cell wall modification, in order to tolerate the stress caused by As [23,24].

As exposure also affects plant secondary metabolism, promoting the synthesis of phenolic compounds, flavonoids, and other metabolites. These metabolites not only act as antioxidants but can also sequester As within the plant, thus minimizing its toxicity [25]. Hyperaccumulator plants possess transport and sequestration systems that allow them to store large amounts of As without suffering damage [8,14]. Although numerous reviews have addressed As toxicity in plants, most have focused on specific aspects such as uptake

and transport, oxidative stress, detoxification mechanisms, phytoremediation, or molecular responses, each treated independently [20,21]. Consequently, there remains a need for a comprehensive synthesis that integrates these processes within a metabolic framework to explain how the initial events of As speciation, uptake, and transport ultimately drive metabolic reprogramming and determine plant adaptation to As stress. In this context, the discussion of As speciation, phosphate transporters, aquaporins, soil microbiota, and mitigation strategies is not intended as a collection of independent topics, but rather as the mechanistic foundation required to understand the origin, progression, and regulation of metabolic alterations. By linking these processes, the present review offers a broader perspective on how metabolic pathways are coordinated in response to As exposure, uptake, and transport, leading to detoxification, physiological adaptation, and mitigation under agricultural conditions. The main objective of this review is therefore to advance the understanding of how metabolic pathways are altered in plants exposed to As, by integrating the physiological, biochemical, and molecular mechanisms that connect As uptake and transport with primary metabolism, redox homeostasis, detoxification, secondary metabolism, nutrient interactions, and adaptive responses. Through this unified mechanistic framework, the review seeks to contribute to the development of more effective strategies for improving crop resilience and mitigating the effects of As contamination in agricultural and environmental systems.

## 2. Arsenic Dynamics in the Environment and Uptake Mechanisms in Plants

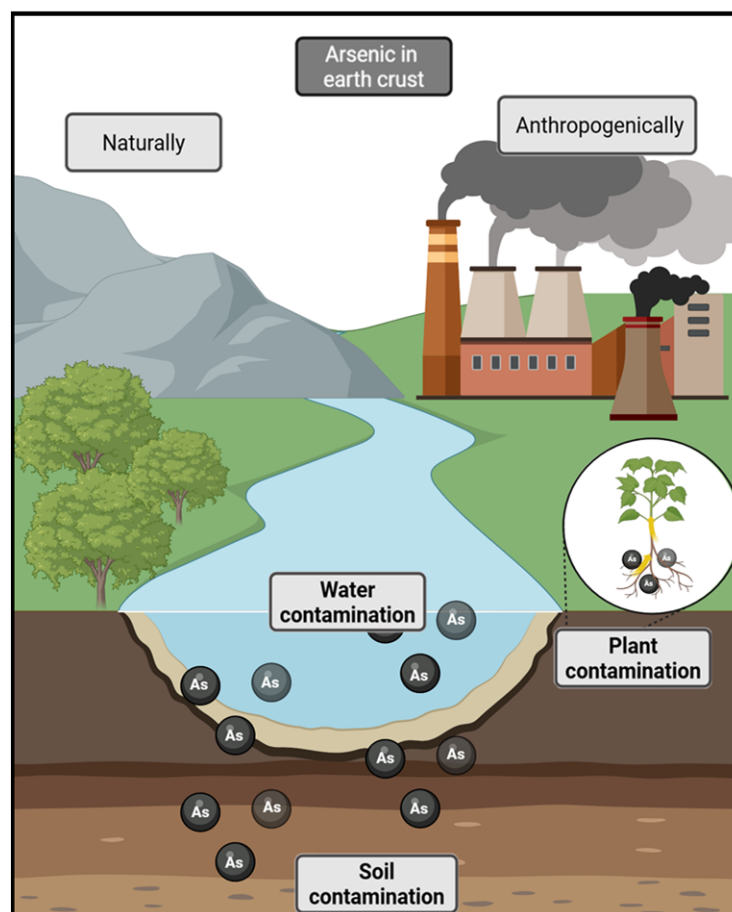
In the environment, As speciation is primarily governed by redox conditions and is further influenced by soil pH and mineral composition [26]. Under oxidizing conditions, As(V) is the predominant inorganic species, whereas As(III) predominates under reducing conditions, such as in waterlogged soils [27,28]. The mobility and bioavailability of both species are further affected by pH-dependent adsorption to soil minerals and by interactions with competing ions such as phosphate and silicate [11,29]. Table 1 summarizes the most common As species in soils under different environmental conditions.

**Table 1.** As speciation in soils at different pH values.

| Oxidation State of As | Species Present | pH         | Reference |
|-----------------------|-----------------|------------|-----------|
| As(III)               | $H_3AsO_3$      | $pH$ 0–9   | [26]      |
|                       | $H_2AsO^{3-}_3$ | $pH > 9$   |           |
|                       | $HAsO^{2-}_3$   |            |           |
| As(V)                 | $H_3AsO_4$      | $pH$ 1–3   | [27]      |
|                       | $H_2AsO^{4-}_4$ | $pH$ 3–6   |           |
|                       | $HAsO^{2-}_4$   | $pH$ 7–11  |           |
|                       | $AsO^{3-}_4$    | $pH$ 12–14 |           |

Therefore, the chemical speciation of As is critical in determining soil toxicity, as well as the mobility of As species and their interaction with plants.

Figure 1 illustrates the natural and anthropogenic release of As from the Earth's crust into soil and water. Once mobilized, As contaminates aquatic and terrestrial environments and can be taken up by plants, facilitating its transfer through the soil–water–plant system [30]. The uptake and accumulation of As in plants cause phytotoxicity [28,31], which is reflected in impaired plant development and reduced crop yields. In addition, As(V) can partially replace phosphate in some biochemical reactions, leading to unstable As(V)-containing intermediates that inhibit shoot formation and root growth.

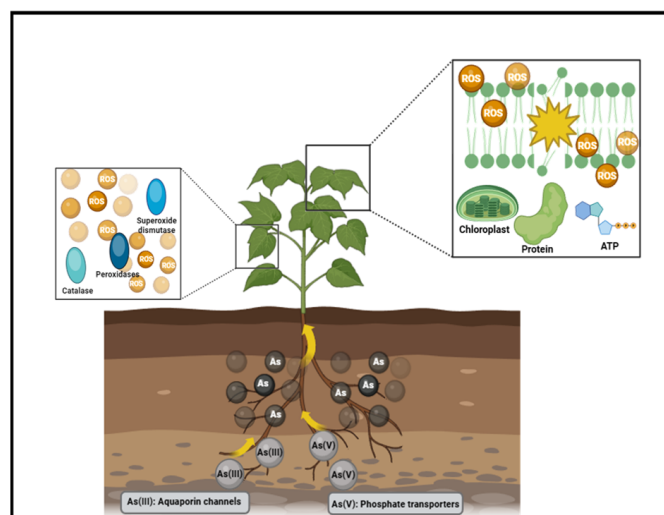


**Figure 1.** As in the environment. As can enter aquatic and terrestrial ecosystems through two routes: natural and anthropogenic. As, arsenic.

As tolerance in plants varies widely and depends on factors such as soil As concentration, pH, organic matter content, microbial activity, and As speciation in water, all of which influence As uptake and toxicity [32,33].

The uptake of As species by plants occurs mainly as As(V), which enters through phosphate transporters located in the root. Because the structure of As(V) is similar to that of phosphate, transporters cannot completely discriminate between the two anions, favoring As(V) uptake [13,28]. Inside the cell, As(V) is reduced to As(III) by the enzyme arsenate reductase (AR); As(III) then affects protein structure and generates ROS that cause oxidative stress [12,20,29]. Once absorbed, most As accumulates in the roots, while the remainder can be translocated to stems and leaves via the xylem [12,20].

Figure 2 illustrates the mobilization of As in plants and the activation of antioxidant defense mechanisms in response to oxidative stress. The activity of antioxidant enzymes (SOD, CAT and POD) increases to help mitigate the damage caused by ROS [22]. In turn, GSH and other non-enzymatic antioxidants accumulate under stress and facilitate As detoxification through its sequestration in vacuoles [9,34,35]. In addition, antioxidants are also produced in plants to regulate ROS concentration, since ROS accumulation can seriously damage cellular processes and ultimately lead to cell death [22]. The antioxidant defense system that controls ROS production in response to As stress involves enzymatic and non-enzymatic compounds [36]. Non-enzymatic antioxidants include reduced GSH, ascorbate, phenols, and flavonoids; whereas enzymatic antioxidants include CAT, POD, and SOD [37]. Increased antioxidant production contributes to As tolerance [38], allowing the plant to survive with some degree of resistance.



**Figure 2.** Effects of As on plants. As, arsenic; As(III), arsenite; As(V), arsenate; ROS, reactive oxygen species.

During As mobilization in the plant, both primary (e.g., photosynthesis, the Calvin cycle, phosphate metabolism, and ATP production) and secondary metabolism (e.g., synthesis of phenols, flavonoids, antioxidant compounds) are affected [15,39,40]. The following sections describe how these metabolic alterations contribute to plant responses under As stress. Primary plant metabolism includes chemical processes that are directly involved in plant survival, growth, and reproduction [15,41]. As shown in Table 2, the compounds involved in these processes include amino acids used for protein synthesis, nucleotides, sugars, and acylglycerols [15,41]. Some of these tend to increase in concentration when the plant is subjected to As stress. For example, proline and other amino acids participate in the synthesis of GSH and of antioxidant enzymes that contribute to the defense of the plant against As. However, when As concentrations are high (>200  $\mu\text{M}$ ), changes in protein content are observed, with total protein concentration decreasing as the As concentration increases [42].

**Table 2.** Effects of As-induced stress on primary metabolites in plants.

| Plant Species                              | Plant Part and Growth Stage  | As Species       | Stress Conditions Due to As                                                                                                                                  | Metabolite               | Stress Response to As                                                                                                   | Reference |
|--------------------------------------------|------------------------------|------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------|-------------------------------------------------------------------------------------------------------------------------|-----------|
| Indian mustard ( <i>Brassica juncea</i> )  | Roots and leaves             | As(V)            | Soil irrigation for 30 and 60 days (0, 100, 300 and 500 mM As(V))                                                                                            | Soluble protein          | At 100 $\mu\text{M}$ , protein $\uparrow$ 67.67% (30 days), $\downarrow$ 60% (60 days) in roots.                        | [43]      |
| Green gram ( <i>Vigna radiata</i> )        | Roots and shoots             | As(III)          | In vitro cultivation for 8 days (0, 0.5, 1 and 2 $\mu\text{M}$ As(III))                                                                                      | Pro                      | At 2 $\mu\text{M}$ , Pro $\uparrow$ 23% in roots.                                                                       | [44]      |
| Horseradish ( <i>Armoracia rusticana</i> ) | Adult roots                  | As(V)            | In vitro cultivation with micropropagation for 7 days (0.02, 0.03, 0.09, 0.14, and 0.19 $\mu\text{M}$ $\text{Na}_2\text{HAsO}_4 \cdot 7\text{H}_2\text{O}$ ) | Pro                      | At 0.02 $\mu\text{M}$ , Pro $\uparrow$ 6.66% in adult roots.                                                            | [41]      |
| Rice ( <i>Oryza sativa</i> L.)             | Leaves and roots (seedlings) | As(III)<br>As(V) | Soil irrigation As(III) (50 and 100 $\mu\text{M}$ ) and As(V) (100 and 500 $\mu\text{M}$ )                                                                   | Proteins (Protein total) | At 500 $\mu\text{M}$ As(V), protein $\downarrow$ 59% in leaves.                                                         | [45]      |
| Soybeans ( <i>Glycine max</i> )            | Roots                        | As(V)            | Soil irrigation for 8 days (25, 50, 100 and 200 $\mu\text{M}$ of $\text{Na}_2\text{HAsO}_4 \cdot 7\text{H}_2\text{O}$ )                                      | Soluble protein          | At 25 $\mu\text{M}$ , protein $\uparrow$ 43% in roots.                                                                  | [42]      |
| Spinach ( <i>Spinacia oleracea</i> )       | Whole adult plant            | As(V)            | Soil irrigation (0, 80.4, 161 and 241 $\mu\text{M}$ of As(V)).                                                                                               | Pro, Glu, Asp, Ala       | At 80.4 $\mu\text{M}$ , Pro $\uparrow$ 4.5%, Glu $\uparrow$ 2.6%, Asp $\uparrow$ 1.3% and Ala $\uparrow$ 3.7% in roots. | [46]      |

Abbreviations:  $\uparrow$ , increase;  $\downarrow$ , decrease; Pro, proline; Asp, aspartate; Ala, alanine; Glu, glutamic acid. Note: As concentrations correspond to the arsenic compound applied in each original study. Concentrations originally reported in mass units (e.g.,  $\text{mg L}^{-1}$  or  $\mu\text{g L}^{-1}$ ) were converted to  $\mu\text{M}$  using the molecular weight of the arsenic compound. Concentrations originally reported in molar units were retained or expressed as equivalent  $\mu\text{M}$  values when appropriate to improve consistency across studies.

On the other hand, secondary metabolites are chemical compounds synthesized by plants that are not essential for survival; therefore, their absence is not lethal [31]. However, as derivatives or by-products of primary metabolism, they can serve as indicators of the ecological interactions of the plant with its environment [47]. Table 3 summarizes the antioxidant and redox responses associated with arsenic stress, including non-enzymatic antioxidants, antioxidant enzymes, oxidative damage indicators, and photosynthetic pigments. These parameters are presented separately from specialized metabolism because they represent distinct physiological processes [12,22,48]. Photosynthetic pigments, such as chlorophyll, are affected by the phytotoxicity caused by As in some plants. As stress can alter the concentration of non-enzymatic antioxidants involved in ROS detoxification [49,50]. In general, As reduces chlorophyll synthesis, although an increase has been observed at low As concentrations ( $<8 \mu\text{M}$ ), followed by a decrease at higher concentrations ( $>8 \mu\text{M}$ ) [30]. This trend could be attributed to the reported stress responses of plants; it has been reported [51] that As species at low doses ( $5 \mu\text{M}$ ) have a stimulatory effect on photosynthetic pigment levels, mainly chlorophyll. However, under As-induced stress, chlorophyll accumulation may have a dual role, since excited chlorophyll molecules can contribute to singlet oxygen ( $^1\text{O}_2$ ) generation under conditions of excess excitation energy. Therefore, photoprotection of photosynthetic structures relies mainly on antioxidant compounds, including carotenoids, tocopherols, ascorbate, glutathione, and phenolic metabolites, which participate in ROS detoxification [50,52].

**Table 3.** Effects of As-induced stress on antioxidant and redox responses, oxidative damage indicators, and photosynthetic pigments in plants.

| Plant Species                              | Plant Part and Growth Stage   | As Species       | Stress Conditions Due to As                                                                                                                                     | Metabolite/Biochemical Parameter        | Stress Response to As                                                                                                                                                                                                                              | Reference |
|--------------------------------------------|-------------------------------|------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------|
| Barley ( <i>Hordeum vulgare</i> L.)        | Seedling and adult plant      | As(V)            | Soil irrigation (0 and $100 \mu\text{M}$ of $\text{Na}_2\text{HAsO}_4 \cdot 7\text{H}_2\text{O}$ )                                                              | SOD, CAT                                | At $100 \mu\text{M}$ , SOD $\uparrow$ 14.18% and CAT $\uparrow$ 19.21% in roots.                                                                                                                                                                   | [53]      |
| Black bean ( <i>Vigna mungo</i> )          | Seeds                         | As(V)            | Soil irrigation (0, 100 and $200 \mu\text{M}$ of $\text{Na}_2\text{HAsO}_4 \cdot 7\text{H}_2\text{O}$ )                                                         | SOD, CAT, POD, APX, Chlorophyll a and b | At $200 \mu\text{M}$ , SOD $\uparrow$ 63%, POD $\uparrow$ 21%, APX $\uparrow$ 23%, CAT $\downarrow$ 28.2%, chlorophyll a and b $\downarrow$ 10.5% in seeds.                                                                                        | [54]      |
| Indian mustard ( <i>Brassica juncea</i> )  | Roots and leaves              | As(V)            | Soil irrigation for 30 and 60 days (0, 100, 300 and $500 \mu\text{M}$ of As(V))                                                                                 | SOD, CAT, POD, APX, GR, MDA             | At $100 \mu\text{M}$ , SOD $\uparrow$ 20.2%, $\uparrow$ CAT, $\uparrow$ 42.3% POD, $\uparrow$ 28.5% APX, $\uparrow$ 9% GR and $\uparrow$ MDA 28%, in 30 day old plants. SOD 22.8% $\uparrow$ and $\uparrow$ GR 24%, in 60 day old plants in roots. | [43]      |
| Corn ( <i>Zea mays</i> )                   | Roots                         | As(V)            | Soil irrigation (0, 50, 100 and $150 \mu\text{M}$ of $\text{Na}_2\text{HAsO}_4 \cdot 7\text{H}_2\text{O}$ )                                                     | Chlorophyll a and b                     | At $100 \mu\text{M}$ , chlorophyll a and b $\downarrow$ 55.8% in roots.                                                                                                                                                                            | [55]      |
| Green gram ( <i>Vigna radiata</i> )        | Roots and shoots              | As(III)          | In vitro cultivation for 8 days (0, 0.5, 1 and $2 \mu\text{M}$ of As(III))                                                                                      | MDA, SOD, CAT                           | A $2 \mu\text{M}$ , MDA $\uparrow$ 32%, SOD $\uparrow$ 45% and CAT $\uparrow$ 50% in roots.                                                                                                                                                        | [44]      |
| Horseradish ( <i>Armoracia rusticana</i> ) | Adult roots                   | As(V)            | In vitro cultivation with micropropagation for 7 days (0.02, 0.03, 0.09, 0.14, and $0.19 \mu\text{M}$ of $\text{Na}_2\text{HAsO}_4 \cdot 7\text{H}_2\text{O}$ ) | CAT, APX, GST, POD                      | At $0.19 \mu\text{M}$ , CAT $\uparrow$ 28.6%, APX $\uparrow$ 50%, POD $\uparrow$ 50%, GST $\uparrow$ 14.28% in adult roots.                                                                                                                        | [41]      |
| Lettuce ( <i>Lactuca sativa</i> L.)        | Adult plant (leaves)          | As(V)            | Hydroponic cultivation for 30 days (0, 1, 2, 8, 12, $16 \mu\text{M}$ of $\text{Na}_2\text{HAsO}_4 \cdot 7\text{H}_2\text{O}$ )                                  | Chlorophyll a and b                     | At $8 \mu\text{M}$ , chlorophyll a $\uparrow$ 54.2%, chlorophyll b $\uparrow$ 48.2% in leaves.                                                                                                                                                     | [30]      |
| Rice ( <i>Oryza sativa</i> L.)             | Seedlings (leaves and shoots) | As(V)            | Soil irrigation for 30 days (0 and $6.43 \mu\text{M}$ of $\text{Na}_2\text{HAsO}_4 \cdot 7\text{H}_2\text{O}$ )                                                 | SOD, CAT, Chlorophyll a and b           | At $6.43 \mu\text{M}$ $\text{Na}_2\text{HAsO}_4$ , SOD $\downarrow$ 34.46%, CAT and chlorophyll a and b in leaves $\downarrow$ 27.3%.                                                                                                              | [56]      |
| Rice ( <i>Oryza sativa</i> L.)             | Roots and shoots              | As(V)<br>As(III) | Soil irrigation As(III) (50 and $100 \mu\text{M}$ ) and As(V) (100 and $500 \mu\text{M}$ )                                                                      | SOD, APX, GR                            | At $100 \mu\text{M}$ As(V), APX $\uparrow$ 28.21% and GR 52%, in roots. SOD $\downarrow$ 32% with As(III).                                                                                                                                         | [45]      |
| Soybeans ( <i>Glycine max</i> )            | Roots                         | As(V)            | Soil irrigation for 8 days (25, 50, 100 and $200 \mu\text{M}$ of $\text{Na}_2\text{HAsO}_4 \cdot 7\text{H}_2\text{O}$ )                                         | APX, SOD                                | At $100 \mu\text{M}$ , APX $\uparrow$ 32% and SOD $\uparrow$ 24% in roots.                                                                                                                                                                         | [42]      |

Table 3. Cont.

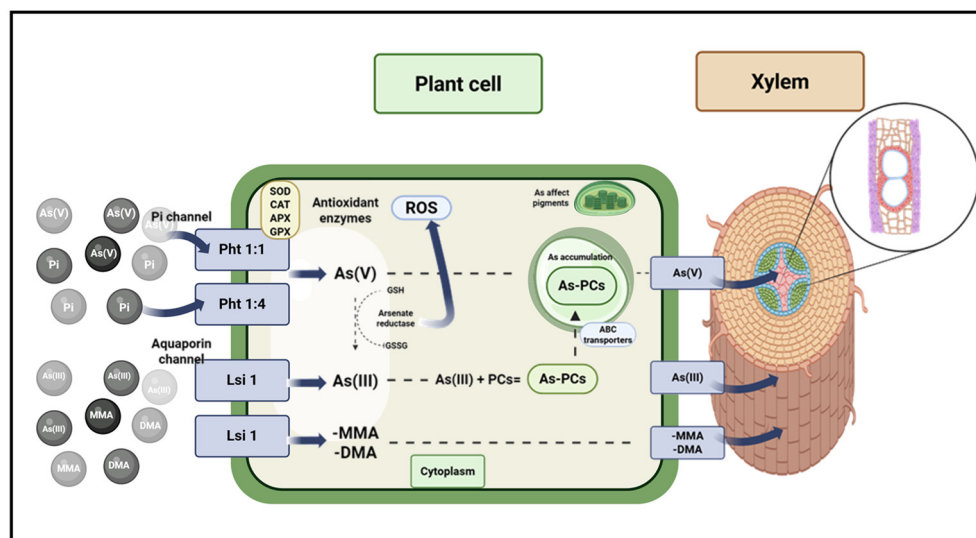
| Plant Species                           | Plant Part and Growth Stage | As Species | Stress Conditions Due to As                                                                                         | Metabolite/Biochemical Parameter         | Stress Response to As                                                                                                         | Reference |
|-----------------------------------------|-----------------------------|------------|---------------------------------------------------------------------------------------------------------------------|------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------|-----------|
| Spinach<br>( <i>Spinacia oleracea</i> ) | Whole adult plant           | As(V)      | Soil irrigation (0, 80.4, 161 and 241 $\mu\text{M}$ of As(V)).                                                      | Chlorophyll a and b, CAT, GPX, APX, SOD. | At 80.4 $\mu\text{M}$ , chlorophyll a and b $\downarrow$ 18%, CAT $\uparrow$ 18%, GPX 2.4%, APX 3.2% and SOD 12.5% in leaves. | [46]      |
| Wheat<br>( <i>Triticum durum</i> )      | Seedlings                   | As(V)      | Soil irrigation (0, 322, 643, 1610 and 2250 $\mu\text{M}$ of $\text{Na}_2\text{HAsO}_4 \cdot 7\text{H}_2\text{O}$ ) | Chlorophyll a and b                      | At 322 $\mu\text{M}$ , chlorophyll a and b $\downarrow$ 60.3% and 39.7%, respectively in leaves.                              | [57]      |

Abbreviations:  $\uparrow$ , increase;  $\downarrow$ , decrease; SOD, superoxide dismutase; GST, glutathione S-transferase; POD, peroxidase; CAT, catalase; APX, ascorbate peroxidase; GR, glutathione reductase; GPX, guaiacol peroxidase; MDA, malondialdehyde. Note: As concentrations correspond to the arsenic compound applied in each original study. Concentrations originally reported in mass units (e.g.,  $\text{mg L}^{-1}$  or  $\mu\text{g L}^{-1}$ ) were converted to  $\mu\text{M}$  using the molecular weight of the arsenic compound. Concentrations originally reported in molar units were retained or expressed as equivalent  $\mu\text{M}$  values when appropriate to improve consistency across studies.

The evidence summarized in Tables 2 and 3 reveals consistent physiological and metabolic patterns that extend beyond individual experimental observations. Although the magnitude of the responses varies according to plant species, As concentration, exposure duration, and experimental conditions, several common trends emerge. Overall, these studies suggest that As(III) often induces more severe metabolic disturbances than As(V), although these responses depend on arsenic concentration, exposure system, uptake efficiency, and plant species. The higher reactivity of As(III) with sulfhydryl groups may contribute to these differences, whereas As(V) primarily disrupts phosphate uptake and energy metabolism before being reduced to As(III) within plant cells. Furthermore, many studies support a hormetic response in which low As concentrations stimulate antioxidant enzyme activities and the accumulation of protective metabolites, whereas higher concentrations exceed the plant's detoxification capacity, leading to inhibition of photosynthesis, impairment of primary metabolism, and reduced growth [58]. Organ-specific differences are also evident. Roots generally represent the primary site of As accumulation and detoxification, exhibiting stronger activation of antioxidant defenses. In contrast, shoots frequently exhibit physiological consequences associated with As exposure, including chlorophyll degradation, reduced photosynthetic efficiency, altered carbohydrate metabolism, and, in some species, arsenic accumulation and detoxification. Likewise, the considerable inter-specific variation suggests that crop tolerance is frequently associated with the ability to restrict As translocation to aerial tissues, maintain redox homeostasis, and activate detoxification mechanisms; however, the relative contribution of these processes varies among species and experimental conditions. In this context, antioxidant enzymes such as SOD, CAT, APX, POD, GPX, and GR should be interpreted both as protective components of the antioxidant defense system and as reliable biochemical markers of oxidative stress, since their induction reflects activation of ROS-scavenging pathways, whereas their decline under severe arsenic exposure indicates that oxidative damage has surpassed the detoxification capacity of plant cells [59–61]. Finally, the close relationship between primary and secondary metabolism suggests that As-induced disruption of photosynthesis, carbon assimilation, phosphate metabolism, and energy production is frequently accompanied by increased accumulation of phenolics, flavonoids, anthocyanins, glutathione, and other antioxidant compounds. Although these observations are consistent with activation of secondary metabolic pathways, direct evidence demonstrating changes in metabolic flux remains limited. Overall, the available evidence supports the view that As tolerance is associated with coordinated adjustments in primary metabolism, antioxidant defenses, and secondary metabolite biosynthesis rather than isolated biochemical responses.

Figure 3 shows As transport within plant cells [13,62]. As(V) is taken up through phosphate transporters (Pht1) because of its structural similarity to phosphate, resulting in

competition for uptake and disruption of phosphate homeostasis [63]. Once inside the cell, As(V) is reduced to As(III) by arsenate reductase (AR), as described earlier. The resulting detoxification and antioxidant responses were described in the previous section.



**Figure 3.** Uptake and accumulation of As in plant cells. P, phosphorus; ROS, reactive oxygen species; MMA, monomethylarsonic acid; DMA, dimethylarsinic acid; ABC transporters, ATP-binding cassette transporters; PCs, phytochelatins.

Furthermore, after reduction, As(III) can be translocated via the xylem to other parts of the plant (stems and leaves) or immobilized in the root by forming complexes with glutathione or phytochelatins [18]. Once the As(III)–PCs complexes are formed, they can be mobilized within the plant by specific transporters. Thus, complexation of As with PCs determines its mobility and enhances plant tolerance, although it does not necessarily increase As accumulation [8,24].

The absorbed As is then translocated to the aerial tissues of the plant through the xylem [10]. In leaves, As(III) can be further detoxified in vacuoles; through this pathway, plants reduce the cellular damage caused by As [64]. However, not all plants have the same As translocation efficiency. Hyperaccumulator species can transport large amounts of As from the roots to the leaves, concentrating it in vacuoles [65]. The accumulation of As in vacuoles helps to avoid toxicity in the cytoplasm, protecting processes essential for plant survival [48].

#### *Species-Specific Responses of Horticultural Crops to Arsenic Stress*

Although the molecular and physiological mechanisms described above are broadly conserved, horticultural crops differ markedly in As uptake, root-to-shoot translocation, and edible-tissue accumulation. In general, leafy and high-surface-area vegetables (e.g., lettuce, spinach, and *Brassica* species) accumulate more arsenic in their edible tissues than fruit vegetables such as tomato, cucumber, and pepper, and members of the Asteraceae and Brassicaceae families show particularly efficient root uptake and translocation [59,66]. Even among leafy vegetables, tolerance varies with the root-to-shoot transfer factor and antioxidant/phytochelatin capacity, following the order garland chrysanthemum > spinach > lettuce [59]. As speciation is also species-dependent: As(III) predominates in the xylem sap of tomato, cucumber, and rice, whereas As(V) predominates in castor, wheat, and Indian mustard [66]. Rice represents a special case, as it takes up As(III) efficiently through the silicon transporters *Lsi1* and *Lsi2* and accumulates As in the grain, which makes it the crop of greatest dietary concern [61]. These differences imply that

mitigation strategies should be crop-specific, and comparative studies among horticultural crops remain scarce.

### 3. Primary Metabolic Alterations in Plants Exposed to Arsenic

As is taken up by plant roots and, once inside the plant, is transported via the xylem to aerial tissues, where it may accumulate or be redistributed through the phloem [14,67]. To reduce its toxicity, plants sequester it in vacuoles or detoxify it through complexes with glutathione or phytochelatins, in processes mediated by transporters such as ABCs [31].

At the level of primary metabolism, As interferes with photosynthesis by damaging photosystems I and II and reducing the activity of RuBisCO, thereby disrupting the Calvin cycle, limiting carbon fixation and sugar synthesis, and impairing ATP production through competition with phosphate [49,63]. Beyond primary metabolism, As also alters aquaporin expression, affecting water transport and cellular homeostasis, which further contribute to plant stress responses [51,52].

#### 3.1. Photosynthesis and the Calvin Cycle

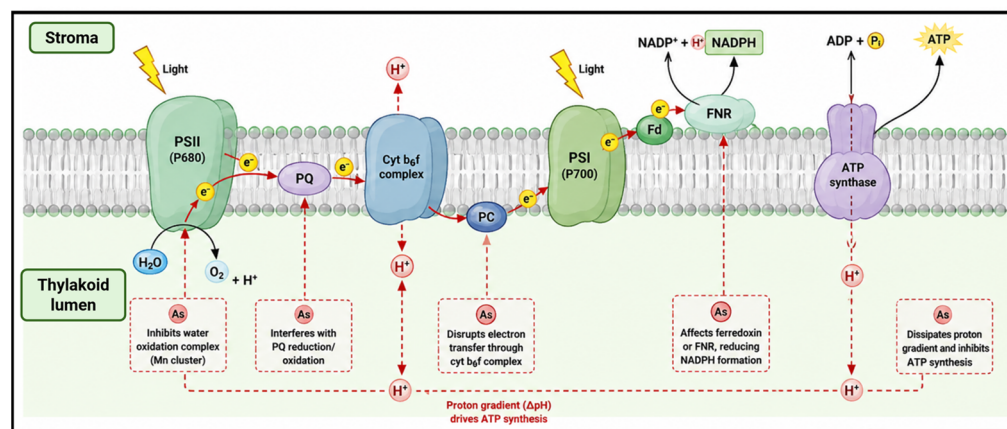
As can negatively affect plant development by altering photosynthetic processes [68]. Photosynthesis comprises two main phases: the light-dependent phase (Figure 4) and the Calvin cycle (light-independent phase; Figure 5) [49]; both phases can be altered in the presence of As. One of the main negative effects of As exposure is the decrease in chlorophyll content, which is closely linked to the efficiency of light absorption [51,52]. Although As has been proposed to interfere with chlorophyll biosynthesis by limiting the availability of magnesium and iron, the relative contribution of this mechanism remains uncertain. Current evidence suggests that the reduction in chlorophyll content observed under As stress is more closely associated with oxidative damage to chloroplast membranes, lipid peroxidation, and impairment of chlorophyll–protein complexes and photosystem II stability than with direct Mg/Fe sequestration [34,65]. Furthermore, phosphate–As(V) competition may disrupt ATP-dependent processes involved in chlorophyll biosynthesis, including Mg-chelatase activity, while oxidative stress and transcriptional changes affecting genes of the tetrapyrrole pathway may further contribute to chlorophyll loss. However, the relative importance of these mechanisms may vary among plant species, arsenic species, and experimental conditions [34,65].

In the light-dependent phase, solar energy is converted into chemical energy in the form of ATP and NADPH. This phase occurs within the thylakoid membrane of chloroplasts [69], specifically in the reaction center of photosystems I and II (PSI, PSII), which are responsible for light absorption and electron exchange. As toxicity can affect this phase of photosynthesis in several ways:

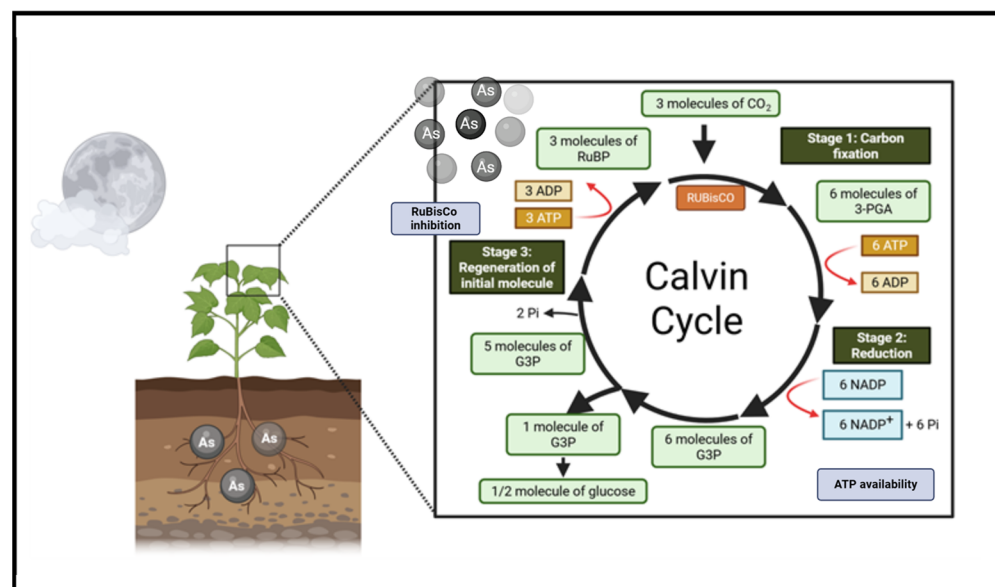
- (a) Damage to photosystems: ROS can oxidize lipids in the thylakoid membrane and damage essential proteins of the photosynthetic apparatus. As induces oxidative stress by generating ROS, which affects the reaction centers of the photosystems [51,69].
- (b) Inhibition of photophosphorylation: As impairs ATP generation and limits the activity of ATP synthase [65,69]. This enzyme produces ATP using the proton gradient across the thylakoid membrane.

On the other hand, during the Calvin cycle (or dark phase), sugars are synthesized from the carbon dioxide fixed by ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO) (Figure 5) [70,71]. This process relies on the products of the light-dependent phase (ATP and NADPH); therefore, any disruption in their generation can significantly affect the efficiency of this pathway. The main changes induced by As in the Calvin cycle include:

- (a) Inhibition of RuBisCO: As can reduce RuBisCO activity by limiting the availability of ATP and NADPH, which are essential for carbon dioxide fixation. As a result, the capacity of the plant to produce sugars from atmospheric carbon decreases [71].
- (b) Reduction of key metabolites: As alters the production of ATP and NADPH, which in turn affects the formation of key intermediates such as 3-phosphoglycerate and glyceraldehyde-3-phosphate, both of which are crucial for carbohydrate biosynthesis [49,72].



**Figure 4.** Effects of arsenic (As) on the photosynthetic electron transport chain during the light-dependent reactions in plants. The diagram represents the thylakoid membrane organization, including the electron flow from water oxidation at photosystem II (PSII) through plastoquinone (PQ), the cytochrome b6f complex, plastocyanin (PC), photosystem I (PSI), ferredoxin (Fd), and ferredoxin–NADP<sup>+</sup> reductase (FNR), leading to NADPH formation. P680 and P700 represent the reaction centers of PSII and PSI, respectively. ADP, adenosine diphosphate; ATP, adenosine triphosphate; NADPH, nicotinamide adenine dinucleotide phosphate (reduced form); Pi, inorganic phosphate. As may disrupt photosynthetic electron transport by affecting PSII activity, electron transfer components, redox balance, proton gradient formation, and ATP/NADPH production, contributing to photosynthetic inhibition under As stress.



**Figure 5.** Effects of As on the Calvin cycle in plants. Pi, inorganic phosphate; RuBP, ribulose-1,5-bisphosphate; ADP, adenosine diphosphate; ATP, adenosine triphosphate; NADPH, nicotinamide adenine dinucleotide phosphate; G3P, glyceraldehyde 3-phosphate; 3-PGA, 3-phosphoglyceric acid.

Even though plants have developed defense mechanisms against As, long-term exposure to this metalloid decreases photosynthetic efficiency, which in turn reduces

biomass production and affects crop growth and yield. Therefore, crops exposed to As-contaminated soils and water face a significant threat to food security in many regions of the world [32,73,74].

At the transcriptional level, As stress also reprograms the expression of photosynthesis-related genes. As-induced oxidative stress alters the transcript and protein levels of chloroplast-encoded genes for core photosynthetic subunits, including *psbA* (encoding the D1 protein of photosystem II), *psaA-psaB* (photosystem I), and *rbcL* (the large subunit of RuBisCO), as well as nuclear genes of chlorophyll biosynthesis, contributing to the decline in chlorophyll content and photochemical efficiency [58,61,75]. In addition, several transcription factor families regulate arsenic-responsive and photosynthesis-associated genes: the *R2R3-MYB* factor *OsARM1* controls As-transporter genes and As tolerance in rice [75], whereas overexpression of the NAC factor *SNAC3* improves arsenic tolerance and grain yield in rice, lowering oxidative-stress markers and preserving gas exchange and chlorophyll content under As stress [58]. These findings link arsenic stress to the transcriptional regulation of the photosynthetic machinery and highlight candidate genes for breeding As-tolerant crops.

### 3.2. Phosphorus Metabolism in Arsenic-Exposed Plants

#### Impact of Arsenic on Phosphorus Uptake

Phosphorus (P) metabolism plays a crucial role in plant metabolic activity, driving ATP generation, nucleic acid synthesis, and the activation of various enzymes. Under As stress, plant metabolism is impaired because oxidative phosphorylation and ATP generation are affected [76,77].

As(V) enters plant roots through  $P_i$  transporters. Under physiologically relevant conditions, As(V) occurs predominantly as  $H_2AsO_4^-$  and  $HAsO_4^{2-}$ , which are structural analogs of the predominant phosphate species  $H_2PO_4^-$  and  $HPO_4^{2-}$ . This structural similarity allows arsenate to compete with phosphate for uptake through  $P_i$  transporters, thereby reducing  $P_i$  acquisition and its availability for cellular metabolic pathways [76,77]. In addition, arsenate can replace phosphate in phosphate-dependent metabolic reactions. This substitution can lead to the formation of unstable arsenate-containing intermediates, thereby disrupting ATP production, DNA synthesis, phosphorylation reactions, and overall cellular metabolism, ultimately contributing to arsenic toxicity [71].

This competition and substitution also disrupt the activity of enzymes involved in the biosynthesis of essential phosphorus-containing compounds [52]. In response to the reduction in intracellular  $P_i$  availability, plants activate phosphate starvation responses, including the induction of phosphatases [22,78]. These enzymes release  $P_i$  from internal organic phosphorus compounds, thereby helping to maintain phosphate levels required for essential metabolic processes [30,69].

Plants take up phosphorus in its inorganic form ( $P_i$ ) by means of specialized transporters located in the plasma membrane of root cells. Members of the *Pht1* family mediate  $P_i$  uptake from the soil solution into root epidermal and cortical cells [79]. Because As(V) is a structural analogue of  $P_i$ , it is transported by these phosphate transporters and competes with  $P_i$  in several metabolic pathways [79,80]. Consequently, the main effects caused on plant metabolism are:

- (a) Disruption of oxidative phosphorylation: the replacement of  $P_i$  by As(V) affects fundamental reactions such as ATP production. Thus, the formation of ADP-As(V) limits the ability to supply energy to plant cells [76].
- (b) Alterations in nucleic acid synthesis: competition of As(V) with  $P_i$  reduces DNA and RNA synthesis, which affects plant growth [77].

In addition to these metabolic effects, As exposure disrupts Pi transport and phosphate homeostasis. Arsenic accumulates in vacuoles and competes with Pi for uptake and distribution, thereby reducing intracellular Pi availability and further limiting phosphate-dependent metabolic processes (Figure 3) [80].

### 3.3. Other Macro- and Micronutrients Affected by Arsenic

Beyond phosphorus, As disrupts the homeostasis of several other macro- and micronutrients. Because As(V) competes with phosphate, phosphorus is the primary target; however, As-induced oxidative damage, altered root architecture, and transporter interference also decrease the acquisition of nitrogen (N), potassium (K), calcium (Ca), magnesium (Mg), iron (Fe), manganese (Mn), zinc (Zn), and copper (Cu). Increasing As exposure has been shown to lower tissue Ca, Mg, Fe, Mn, Zn, and Cu concentrations [60,61]. Sulfur nutrition is especially relevant because it is directly coupled to As detoxification: sulfur assimilation supplies the cysteine required for glutathione and phytochelatin synthesis, and sulfur supply modulates the expression of arsenic transporters and thiol metabolism in rice [61]. Conversely, an adequate supply of some nutrients, such as calcium and silicon, can partially mitigate As accumulation. This multi-element perspective indicates that As toxicity should be interpreted as a broader nutrient-imbalance syndrome rather than a phosphorus-specific effect.

## 4. Role of Aquaporins in the Response to Arsenic Stress

Aquaporins are membrane proteins that selectively facilitate the movement of water and small solutes across cell membranes [77,81]. These proteins play a crucial role in the transport of As in plants and other living organisms, particularly when As is present in its inorganic forms. Aquaporins are channels composed of six  $\alpha$ -helices embedded in the cell membrane, which form a central pore through which water and other small solutes flow [26,82]. Within this pore, certain aquaporins, especially those belonging to the subfamily of NOD26-like intrinsic proteins (NIPs), show affinity for As(III) transport and are grouped into three subgroups according to their pore structure: (a) NIP I: permeable to water, lactic acid, and glycerol [83]; (b) NIP II: possesses larger pores, allowing the transport of molecules such as urea, boric acid, and formamide [45,83]; and (c) NIP III: specialized in the transport of silicic acid.

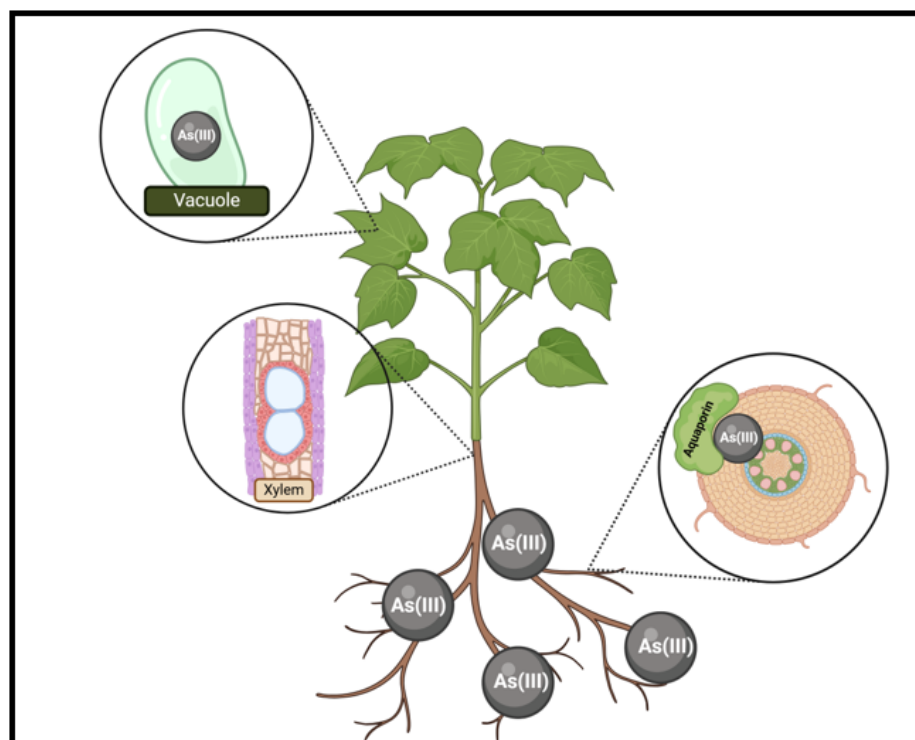
NIPs are particularly involved in the transport of metalloids such as As and Si, as well as of water [74]. The ability of aquaporins to transport water and low-molecular-weight molecules is determined by the structure of their pore [75]. Only a limited number of aquaporins have been identified as capable of transporting As(III), which can be attributed to two main factors. First, the contribution of many aquaporins to arsenic accumulation is less evident than that of well-characterized members such as *OsNIP2;1* and *AtNIP1;1*, making their identification through molecular and genetic approaches more challenging. Second, the high sequence similarity among aquaporins results in considerable functional redundancy, so the loss of a single member often has little measurable effect on arsenic accumulation.

Figure 6 shows the transport of As in plants, which involves several key steps from uptake in the soil to translocation to the aerial parts of the plant:

- (a) Root uptake: As(V) is structurally analogous to phosphate and is mainly taken up through phosphate transporters (Pht). In contrast, As(III) is primarily absorbed by NIP aquaporins located in root cells, facilitating its entry and radial movement through the cortex toward the vascular tissues [84,85].
- (b) Movement into the xylem: Following uptake by root cells, As(III) is transported toward the vascular tissues through radial transport pathways. Subsequent xylem loading

and long-distance translocation involve multiple transport processes, including the participation of additional transporters, rather than aquaporins alone [13].

- (c) Translocation to aerial tissues: Once loaded into the xylem, arsenic is translocated to stems and leaves through the transpiration stream. In aerial tissues, arsenic may be detoxified by complexation with thiol-rich compounds such as phytochelatins and subsequently sequestered into vacuoles, thereby reducing its phytotoxic effects [33,86].



**Figure 6.** Uptake and transport of As(III) through aquaporin channels in plants.

Related to this, recent studies indicate that As exposure is associated with the differential regulation of aquaporin gene expression, which limits the toxic effects of As [12,13,87]. In addition, some plants have developed adaptive mechanisms that reduce As uptake by regulating aquaporin activity under stress [8,31,67]. That is, under combined water stress and As toxicity, aquaporin activity is either enhanced or restricted, depending on the need to balance water uptake against the entry of the toxicant [21,23,24]. This response is mediated by the differential regulation of aquaporin expression or activity in roots and other tissues subjected to stress, and it also contributes to water homeostasis and As detoxification [28,88].

## 5. Potential Applications for Improving Crop Production and Mitigating the Effects of Arsenic Contamination in Ecosystems

The presence of As in agricultural soils represents a persistent environmental threat, especially in regions where irrigation with contaminated water is common [11,82]. In response, sustainable strategies have been developed that seek not only to mitigate As toxicity but also to maintain agricultural productivity. For example, the use of amendments such as biochar has been shown to reduce As mobility, improve soil properties, and favor beneficial microbial activity, resulting in lower As concentrations in plants and better yields [32,89]. In addition, water management techniques such as alternate wetting and drying irrigation in rice have reduced As accumulation in the grain by up to 66%, while

lowering methane emissions and maintaining yields, representing a climate-smart and economically viable practice [90].

Another promising alternative is the use of microbial biofertilizers such as *Bacillus* spp. strains, which, when applied together with agricultural residues, have significantly reduced As accumulation in vegetables without compromising productivity [91,92]. It has also been reported that phytoremediation systems with energy crops or hyperaccumulator species such as *Pteris vittata*, combined with commercial crops, offer the possibility of progressively decontaminating soils without stopping agricultural activity, which opens new opportunities to rehabilitate affected lands with economic benefits [93]. These integrated strategies provide viable solutions at the field level and offer a basis for understanding how As interacts with plant metabolic pathways involved in defense, adaptation, and physiological resilience.

Although each mitigation strategy has demonstrated effectiveness in reducing As toxicity, their applicability varies depending on environmental conditions, crop species, and management practices. Soil amendments such as biochar and silicon provide rapid improvements in As immobilization and soil quality; however, their effectiveness depends on soil characteristics and application rates. Water management strategies are particularly effective in paddy rice systems but are less applicable to upland crops [60,66]. Likewise, microbial biofertilizers represent an environmentally friendly approach that enhances nutrient acquisition and plant tolerance, although their performance may vary under field conditions due to differences in soil microbial communities and environmental factors. In contrast, phytoremediation offers a sustainable long-term solution for remediating contaminated soils but generally requires extended periods before significant reductions in soil As concentrations are achieved [58,59]. Therefore, integrating agronomic practices with advances in molecular breeding and multi-omics technologies may provide the most effective long-term strategy for developing arsenic-tolerant crops while ensuring sustainable agricultural production.

#### *Crop Rotation and Intercropping*

Complementary agronomic practices such as intercropping and crop rotation also offer practical means to reduce arsenic stress in the field. Intercropping edible crops with As hyperaccumulators, particularly *Pteris vittata*, follows a “production while remediation” logic: the hyperaccumulator concentrates As in its own tissues while lowering arsenic in the edible parts of the companion crop. Field and microplot studies have reported large decreases in the As concentration of maize grain when maize is intercropped with *P. vittata*, together with improved nitrogen and phosphorus status and maintained yield [60,66]. Crop rotation (e.g., oilseed rape–rice systems) and the return of green manure can likewise shift As speciation and rhizosphere activity toward immobilization, lowering As accumulation and oxidative-stress markers in the subsequent crop. Because these approaches act mainly through niche separation of root systems, rhizosphere immobilization, and improved nutrient status, they represent economically viable, field-scale complements to the metabolic and genetic strategies discussed in this review.

## **6. Influence of Arsenic on the Soil Microbiota and Consequences for Plant Nutrition and Performance**

As in agricultural soils acts as a strong selective pressure on the soil microbiota, reshaping both its composition and its function. Under As contamination, bacterial and fungal diversity declines. The most affected groups include plant growth-promoting rhizobacteria (PGPR), arbuscular mycorrhizal fungi (AMF), and non-resistant symbiotic bacteria

and fungi. In parallel, arsenic-tolerant taxa become more abundant, such as *Rhizobiaceae*, *Cupriavidus*, *Acidithiobacillus*, *Ralstonia*, *Burkholderia*, and some *Actinobacteria* [87,88].

This enrichment of tolerant taxa plays a central role in As speciation. These microorganisms carry genes of the As cycle, including *ars*, *aio*, *arr*, and *arsM* [87,88]. Through these genes they oxidize, reduce, methylate, and demethylate As. In doing so, the microbiota governs the speciation and mobility of As in the rhizosphere, which in turn determines how much becomes bioavailable to plants [89,90]. The interaction is reciprocal: As-stressed plants release root exudates that reshape the rhizosphere community, favoring microorganisms able to transform or immobilize the metalloid.

These community shifts have direct consequences for plant nutrition. In contaminated soils, beneficial microorganisms are displaced, including PGPR (*Pseudomonas*, *Bacillus*, *Azotobacter*) and AMF (*Glomus*, *Rhizophagus*, *Claroideoglomus*, *Gigaspora*), which normally drive phosphorus solubilization and biological nitrogen fixation [89]. Because As(V) competes with phosphate at root membrane transporters, the loss of phosphorus-solubilizing microbes deepens phosphorus deficiency and limits plant growth. Consistent with this, soil sterilization or microbial disturbance increases the accumulation of inorganic As in aerial tissues of crops such as maize, lowering biomass and causing manganese and phosphorus deficiencies [89,90].

Not all microbial interactions are detrimental. Some endophytic and rhizospheric microorganisms mitigate arsenic stress through two complementary mechanisms. First, certain bacterial consortia immobilize arsenic by oxidizing As(III) to As(V), or by biosorption and precipitation, thereby lowering its availability to plants [87,88]. Second, fungal and bacterial species, including PGPR, produce siderophores, indole-3-acetic acid, and ACC deaminase, which sustain plant growth under stress [91]. In rice, silicon application illustrates both effects: it reduces As accumulation in roots and shoots and shifts the rhizosphere community toward groups linked to greater resilience and antioxidant activity [83,91].

Overall, As-induced changes in the soil microbiota affect plant nutrition in two ways: they reduce nutrient availability and uptake, and they increase the translocation of inorganic arsenic into edible tissues. Conserving indigenous microbiota or introducing beneficial consortia, combined with amendments such as biochar or Fe/Si nanoparticles [92,93], is therefore a promising strategy to reduce As mobility and improve plant performance in contaminated soils. A key knowledge gap remains regarding the function of As-tolerant microbiomes; multi-omics approaches are needed to clarify their resilience mechanisms and guide their agricultural application [92].

## 7. Conclusions

This review highlights that As toxicity in plants results from the integrated disruption of metabolic and physiological processes rather than from isolated biochemical responses. Arsenic uptake and transport, mediated mainly by phosphate transporters and aquaporins, trigger disturbances in primary metabolism, including impaired photosynthesis, energy imbalance, and altered nutrient acquisition. These changes are accompanied by modifications in specialized metabolism and antioxidant defenses, which contribute to plant acclimation or toxicity depending on stress intensity and duration. Moreover, interactions with soil and rhizosphere microbiota further influence As mobility, speciation, and nutrient availability, shaping plant responses under arsenic stress. Therefore, understanding As tolerance requires a holistic approach that integrates plant metabolism, molecular regulation, and plant-microbiome interactions. Future research combining multi-omics approaches, genetic improvement, and sustainable soil-based strategies will be essential for developing As-tolerant crops and promoting agricultural sustainability in contaminated environments.

## 8. Future Perspectives

Building on this integrated view, we identify three priority research directions:

- (i) Metabolic and regulatory networks. Future work should resolve the cross-talk between primary and secondary metabolic pathways under As stress and identify the regulatory nodes—particularly transcription factors such as *OsARM1* and *SNAC3*—that govern tolerance, using integrated transcriptomic and metabolomic (multi-omics) approaches.
- (ii) Genetic improvement and biotechnology. Comparative genetic analyses across crop species, combined with gene-editing and other biotechnological tools, should be used to develop As-tolerant, low-accumulating cultivars—for example, by tuning uptake and translocation transporters (e.g., *Lsi1/Lsi2*) and detoxification (glutathione/phytochelatin) pathways.
- (iii) Rhizosphere and agronomic management. The functional characterization of As-tolerant microbiomes through multi-omics, together with field-scale evaluation of agronomic practices (intercropping with hyperaccumulators such as *P. vittata*, crop rotation) and soil amendments (biochar, Fe/Si nanoparticles), should be prioritized to immobilize arsenic and improve crop performance under real field conditions.

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## Abbreviations

The following abbreviations are used in this manuscript:

|         |                           |
|---------|---------------------------|
| As      | Arsenic                   |
| As(V)   | Arsenate                  |
| As(III) | Arsenite                  |
| ROS     | Reactive oxygen species   |
| SOD     | Superoxide dismutase      |
| CAT     | Catalase                  |
| APX     | Ascorbate peroxidase      |
| GR      | Glutathione reductase     |
| GSH     | Glutathione               |
| GST     | Glutathione S-transferase |
| POD     | Peroxidase                |
| GPX     | Guaiacol peroxidase       |
| MDA     | Malondialdehyde           |
| Pro     | Proline                   |
| Asp     | Aspartate                 |
| Ala     | Alanine                   |
| Glu     | Glutamic acid             |
| ADP     | Adenosine diphosphate     |
| ATP     | Adenosine triphosphate    |

|         |                                             |
|---------|---------------------------------------------|
| Pi      | Inorganic phosphate                         |
| Pht1    | Phosphate transporters                      |
| ABC     | ABC transporters                            |
| PCs     | Phytochelatin                               |
| MMA     | Monomethylarsonic acid                      |
| DMA     | Dimethylarsonic acid                        |
| NADPH   | Nicotinamide adenine dinucleotide phosphate |
| RuBP    | Ribulose-1,5-bisphosphate                   |
| G3P     | Glyceraldehyde 3-phosphate                  |
| 3-PGA   | 3-phosphoglyceric acid                      |
| PQ      | Plastoquinone                               |
| b6f     | Cytochrome b6f complex                      |
| PC      | Plastocyanin                                |
| Fd      | Ferredoxin                                  |
| FNR     | Ferredoxin–NADP <sup>+</sup> reductase      |
| AR      | Arsenate reductase                          |
| Ls1–Ls2 | Silicon transporters                        |
| NIPs    | Nodulin 26 Intrinsic Proteins               |

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