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Vanadium Uptake and Toxicity in Plants

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Abstract

Metal pollution is a global issue in recent times with documented cases of contamination adjacent to mining areas, industries and wastes from agricultural sector. Among all non-essential metals, vanadium is becoming the focus of attention for the environmentalists and plant scientists, since its level in soil, water and atmosphere is gradually increasing day by day, because of several anthropogenic activities, such as burning of fossil fuels, fertilizer and pesticide application and recycling of domestic wastes. Vanadium pentoxide (V_2O_5) is the most commonly existing and usable form of vanadium, along with ammonium metavanadate (NH_4VO_3), sodium metavanadate ($NaVO_3$) and sodium orthovanadate (Na_3VO_4). Because of its mobile nature, vanadium is readily taken up from the soil by the plant roots where it gets immobilized, with only a small fraction being translocated to the above ground organs. Although vanadium, like other trace elements, have been found to stimulate certain physiological processes and improved growth and yield of plants at lower concentrations, its essentiality as minor element is still debated. On the contrary, massive bioaccumulation of vanadium within plant tissues beyond the threshold limit is reported to exert severe consequences like inhibition of growth of plant and plant parts, chlorophyll content and photosynthesis, as well as bringing forth oxidative damages, chromosome breakage and aberrations, disruption in mineral homeostasis and perturbing smooth operation of several metabolic processes. The present review illustrates the progress in vanadium research made so far to understand the mechanism of vanadium uptake and extent of phytotoxicity, which may help in regulating vanadium tolerance in different plant species.

Keywords: Metal pollution; Uptake; Growth inhibition; Metabolic imbalance; Oxidative damages

Introduction

Contamination of agricultural land with metals like cadmium, arsenic, lead, nickel, mercury, copper, etc., detrimental to plant and animal world is a rising concern globally due to rapid industrialization and reckless anthropogenic activities. In addition to these metals, vanadium ranks top five in abundance among transition elements and is naturally found (0.01%) on earth's crust (159 g t^{-1} and 0.14 mg kg^{-1}) particularly in limestone soils with more than 65 different minerals, mostly with iron oxide, argillaceous minerals, carnotite, chileite, bravoite, roscoelite, patronite, vanadinite, davidite and organic fractions [1]. It is distributed in the lithosphere in the range $10\text{--}220 \text{ mg kg}^{-1}$, and mean concentration of 150 mg kg^{-1} in soil, $1.8 \mu\text{g L}^{-1}$ in sea water and 1000 ng m^{-3} in urban areas [2]. The natural deposits of vanadium also include titaniferrous magnetites, shales, certain deposits of phosphate rock, some uranium ores and asphaltic deposits. About 8.4 t of vanadium are emitted from natural sources to atmosphere per annum. The natural sources included volcanoes, continental dusts, forest fires, sea salt spray and biogenic practices [3]. The emissions from petrochemical industries, steel industries, phosphorite treating factories, burning of fossil fuels and industries like mining, metallurgy and galvanization are the major sources of vanadium, which is taken up by the soil particles [4]. Use of heavy oils, tar sands and bitumen as combustion sources lead to increased vanadium amounts in the atmosphere which causes kidney diseases in humans. Modelled air stack emissions from coal combustion suggest that 90% of the vanadium released from this source can be in the form of toxic vanadium pentoxide which may range from 1–18% in the fine ashes suspended in air. Moreover, vanadium loading in environment could be originated from vanadium-containing fertilizers, mine-tailing leachates, and municipal and industrial sludge. It is predicted that more than 60 thousand tons of vanadium is released into the atmosphere each year as the result of anthropogenic activities (mostly combustion of fossil fuels). Surface water and ground water are also contaminated by vanadium mostly due to mining. According to the study conducted in the USA, 0.33 mg L^{-1} is accepted as the safe limit for vanadium in drinking water [5]. Recent

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ecotoxicological reports have placed vanadium among the dangerous pollutants, in the same class as mercury, arsenic and lead. The U.S. Environmental Protection Agency put vanadium on the top list of candidate contaminants [6].

Vanadium pentoxide (V_2O_5) is the most commonly existing and usable form of vanadium, along with ammonium metavanadate (NH_4VO_3), sodium metavanadate ($NaVO_3$) and sodium orthovanadate (Na_3VO_4). Several reports indicate that vanadium mobility, transport, toxicity, bioavailability, and bioaccumulation depend upon its two oxidation states, viz., tetravalent and pentavalent forms, of which the latter is more mobile, active in the vanadium biogeochemical cycle, and exhibits higher toxicity to both plants and animals [7]. The oxidative forms of vanadium have higher harmful effects than the elemental form. Vanadium concentrations higher than a certain level have toxicity to animals (1 ppm for rat; 0.68 ppm for heifer) and humans (10 ppm per day per kg body mass). The ecotoxicological effects of vanadium include various biochemical alterations related to enzymatic activity, interaction with protein, and protein-DNA unit of living organisms and plants. Even then, the Environmental Protection Agency (EPA) of US has not listed vanadium as a pollutant requiring urgent research and legislation, since there is not much evidence about the toxic risk on population, either because of deficiency or overexposure. However, many other countries like Canada (130 mg kg^{-1}), Netherlands (42 mg kg^{-1}), Slovenia (120 mg kg^{-1}), and Czech Republic (180 mg kg^{-1}) have developed guidelines that can be used to assess toxicity for vascular plants and soil invertebrates, based on community responses [8]. The tetravalent form can incorporate into a mineral crystal that is comparably less mobile and was indicated to be the major component in soil. The mobility of tetravalent form is more likely linked to chemical and biological weathering processes.

Vanadium Uptake by Plants

It was earlier reported that pH has effect on vanadium absorption by roots *via* (a) changes in ionic forms of vanadium in solution, and (b) OH^- inhibition of vanadium uptake, e.g., the rate of vanadium uptake was highest at pH 4, but dropped to very low level at pH 10. The uptake is not dependent on expenditure of metabolic energy by the roots. The vanadates (compounds containing an oxanion of vanadium) can be taken up by plants in place of phosphate, and can be mobilized in nitrogen poor soil by nitrogen-fixing organisms, such as *Azotobacter vinelandii* [9], thus making them available for plant uptake. During uptake by plant roots, biotransformation of vanadium occurs, which involves reduction of pentavalent vanadium that readily oxidizes aldehydes, ketones, catechols, olefins and sulphydryls found in cell wall even at pH 7. Vanadium is therefore strongly retained by the root tissues and undergoes ready reduction to the tetravalent form. This reduction leads to immobilization of vanadium within the root tissues. Soil properties also affect the fate of vanadium in soil and hence uptake. Iron and aluminium hydroxides determine vanadium mobility in soil and water [10]. In case of *Lycium* seedlings, vanadium interacted with polysaccharides and acid-soluble polar compounds on cell wall in stem and leaf, whereas with pectin and cellulose in roots, which reduced vanadium damage due to their antidotal effect [11]. Tian et al., (2015) [12] observed in rape (*Brassica juncea* L.) that vanadium accumulated in the sequence: root>stem>leaf>seed, with only a small fraction being translocated to the above ground organs.

Toxicity of Vanadium in Plants

Vanadium is a trace element playing highly critical role in

biochemical processes. Vanadium is essential for life particularly in aquatic ecosystems where it is utilized by ocean algae as an active centre of the haloperoxidase enzymes [13]. Vanadium acts as a growth promoting factor at lower levels that supports nitrogen fixation in molybdenum-deficient soil, stimulate chlorophyll production, show insulin-mimetic activities in humans, facilitate tumor therapy, and serve as an essential element for some animals in trace amounts. Vanadium was recorded in various commercial nutritional supplements and multivitamins in amounts ranging from 0.0004 mg to 12.5 mg. Some perennial plants and mushrooms have proven to be extremely rich in this element [14]. However, the essentiality of vanadium for higher plants and crops is yet to be unequivocally accepted by the biologists and biomedical scientists. Because of the structural analogy between vanadate and phosphate, the consumption of vanadium-enriched contaminated grass by mammals can replace phosphates in their bones [15]. The growth of plants can be stimulated by trace quantities of vanadium (1-10 $\mu g L^{-1}$), but concentrations (100 $\mu g L^{-1}$) were found to be toxic [16]. Usually, the concentration of vanadium in plants is positively correlated with that in soil.

Inhibition in growth of plant and plant parts

Vanadium concentration above 2 ppm exerts toxic effects in plants by causing oxidative stress, growth inhibition, leaf chlorosis and necrosis, coraloid root structure and suppression in the uptake of different essential elements [17]. The application of a high vanadium dose (120 μM) in Triticale ($\times$ *Triticosecale* Wittm.) inhibited shoot growth [18]. Root growth inhibition in rice and chickpea was noted at 1 mM and 60-120 mg L^{-1} vanadium [19,20]. Application of 80 mg L^{-1} vanadium affected plant height and stem diameter in rice [21]. About 170-1180 μM vanadium in chickpea caused leaf deformities and size decrease as the concentration of applied vanadium increased [22]. The seedling growth, fresh and dry biomass of root and shoot, and tolerance index in chickpea seedlings were all linearly decreased with increasing vanadium concentrations (130, 170 and 200 mg kg^{-1}), with more significant accumulation of vanadium in roots than shoots, showing that translocation from root to shoot was low [23,24]. The weight of fresh root biomass was decreased significantly in chickpea with the application of 25 mg L^{-1} vanadium [25]. The roots of swamp morning glory (*Ipomoea aquatica*) turned thicker and darker with decreased growth because of the accumulation of the toxic pentavalent vanadium [26]. In Chinese green mustard (*B. campestris* ssp. *chinensis* var. *parachinensis*), vanadium level up to 80 mg L^{-1} decreased plant height and number of leaves [27]. Not only that, the weight of fresh root biomass decreased with the increase in the concentration of the applied vanadium [28]. The treatment of the plants with various concentrations of vanadium (20-100 mg L^{-1}) significantly reduced growth and development of shoots and roots in mustard (*Brassica juncea* var. *gracilis*), along with inhibited lateral root development [29]. The root and leaf growth in lettuce (*Lactuca sativa*) was inhibited by doses of 0.5 to 1.0 mg kg^{-1} vanadium, along with loss of leaf turgidity, mild chlorosis and decrease in yield. The main root turned club-shaped, dark-colored and necrotic, together with the reduction in secondary root length and number [30]. The application of 15-153 μM vanadium inhibited the formation of secondary roots in cuphea [31], while 160-400 μM vanadium in bean plants grown hydroponically caused lesser growth of the main root and a lower number of secondary roots. The leaf length and leaf area also decreased significantly as the vanadium concentration increased, starting at 240 μM vanadium [32]. The decrease in leaf growth might be related with the decrease in activity of the enzymes, nitrate reductase and transaminase, involved in the synthesis of amino acids

[33]. The dry biomass of stems and roots of soybean plants (*Glycine max*) significantly decreased when vanadium concentration exceeded 30 mg kg⁻¹ in the soil solution [34]. High concentrations of vanadium postponed the germination, growth and biomass of the soybeans, with productions being half at 500 mg kg⁻¹ spiked vanadium. Vanadium mostly accumulated in the roots with <20% transported to the aboveground parts [35]. In case of pepper (*Capsicum annuum*) plants, it was shown that 15 μ M vanadium retarded plant growth, lowered the stem diameter and number of leaves per plant, reduced the leaf area and fresh and dry biomass of leaves, roots and stems, and developed toxicity symptoms like lowering of leaf chlorophyll, as compared to 5 μ M vanadium which stimulated plant growth and leaf chlorophyll formation, induced floral bud development, and accelerated flowering [36]. Vanadium application (50 mg L⁻¹) reduced both the fresh and dry weight of watermelon seedlings by up to 57% and 48%, respectively, and adversely affected root growth by reducing total root length, root volume, root surface area, root forks, root tips and root crossings [37]. Aihemaiti et al. (2019) [17] observed that vanadium concentration of 40 and 55.8 mg L⁻¹ in soil solution causes a 50% decrease in root length and stem height respectively in dog tail's grass (*Setaria viridis*), indicating that root length is more susceptible to vanadium toxicity than stem growth. The threshold values of vanadium for stem height and root length were 36.8 and 16.3 mg L⁻¹ respectively.

Inhibition in chlorophyll synthesis and photosynthetic parameters

It was observed in swamp morning glory that the application of 0.5-2.5 mg L⁻¹ vanadium caused decrease in the concentrations of chlorophyll a and b as the vanadium concentrations increased [26]. The concentration of chlorophyll a and b and total carotene in chickpea was also decreased as the vanadium levels increased (15-120 mg L⁻¹) [20]. A decrease in the number of chloroplasts in common bean was reported in cells at concentrations of 240 and 320 μ M [32]. Vanadium at 10 mM concentration decreased chlorophyll concentration in sugar beet (*Beta vulgaris* L. subsp. *vulgaris* var. *altissima*) [38]. Relative chlorophyll content index and leaf photosynthetic parameters like photosynthetic assimilation, stomatal conductance, intercellular CO₂, and transpiration were drastically reduced together with lowered *chlorophyll synthase* gene expression in watermelon upon application of vanadium at 50 mg L⁻¹ [37]. The vanadium treatments resulted in significant reductions in the photosynthetic parameters in mustard including net photosynthetic rate, stomatal conductance and transpiration rate (Tr) [24]

Inciting oxidative damages

The Reactive Oxygen Species (ROS) and atmospheric oxygen are the integral agents to oxidize the vanadium compounds to +5 oxidation state in the cells which reduced to +4 oxidation state by the action of intracellular antioxidant. Vanadium application at 25 mg L⁻¹ to chickpea plants substantially increased the H₂O₂ and Malondialdehyde (MDA) content [20]. Likewise, H₂O₂ and MDA levels were also enhanced in the root and leaf tissues of watermelon seedlings at vanadium concentration of 50 mg L⁻¹ along with enhancement of the transcript abundance of *respiratory burst oxidase* genes. In addition, vanadium-dependent *haloperoxidase* gene expression was also activated due to increased vanadium accumulation in the leaves, stem and root [37], that altogether caused severe oxidative damages. H₂O₂ production in chickpea seedlings was prominent at higher vanadium concentration (170 and 200 mg kg⁻¹), which highly activated the antioxidative enzymes like Superoxide

Dismutase (SOD), Catalase (CAT) and Peroxidase (POD). The up regulated SOD activity was attributed to de novo synthesis of enzyme protein. The CAT activity enabled elimination of H₂O₂ and POD protected cellular membranes against oxidative damages. The ROS generated initiated a cyclic cascade of reactions which disrupted the lipid bi-layer of the membrane and distorting the membrane by the Fenton reaction. The cell death and ion leakage (indicating membrane disruption) were also positively increased with increase of vanadium levels. Vanadium concentrations of 80 and 100 mg L⁻¹ resulted in a pronounced increase in SOD, CAT and POD enzyme activities probably due to the generations of additional levels of ROS that result from increased oxidative damages. The tetravalent vanadium stimulates ROS to hinder the antioxidative machinery. The oxidation of tetravalent to pentavalent form is also initiated by the generation of hydroxyl radicals through Fenton-like reaction [39].

Early studies showed that vanadium caused G2/M cell cycle arrest through ROS-mediated reactions [40]; it mimicked growth factor activities by inhibiting tyrosine phosphatases and had inhibitory or stimulatory effects on the activities of receptor and non-receptor protein tyrosine kinases, depending on the oxidation state [41]. Around 28 ROS network genes, belonging to class III peroxidase, monodehydroascorbate reductase, glutathione reductase, glutaredoxin and thioredoxin (Trx), and Glutathione S-transferase (GST), were found to be induced by vanadium stress in rice [19]. Pronounced decrease in protein contents and anthocyanin contents were also observed at such vanadium concentrations [23,24]. Protein contents also showed decreasing trend in chickpea as the vanadium concentrations increased from 15 to 120 mg L⁻¹ [20]. Vanadium absorbed by rice plants greatly inhibited chlorophyll biosynthesis and interfered with sulfur-containing amino acids and crude protein, which resulted in decreased protein content. Vanadium oligomers interact with several proteins and affect numerous biological mechanisms, such as membrane-bound transport systems, depending on the oligomeric species present. Excess vanadium increased lipid peroxidation and markedly increased Mitogen-Activated Protein Kinase (MAPK) and Calcium-Dependent Protein Kinase (CDPK) activity in rice roots [19].

Disruption in the endogenous level of essential and trace elements

Vanadium acts as a phosphate analog, interfering with various vital enzymatic systems involved in phosphorus metabolism, inhibiting the activity of different phosphatases, ATPases, ribonucleases and protein kinases, while activating NADPH oxidase and inducing genotoxicity and mutagenic effects [42,43]. The increasing levels of vanadium up to 2.0 mg kg⁻¹ decreased the P concentrations in soybean plants [34]. The same result was shown in swamp morning glory where the P concentration decreased in leaves, stems and roots with increase in vanadium concentration [32], thereby inhibiting the activity of enzymes in which P is an important component, like phosphatases, ligases, synthases and ATPases [44,45]. Pepper plants treated with 15 μ M vanadium showed symptoms of K deficiency and decreased the concentrations of Mg and Mn in leaves [36]. Application of vanadium substantially reduced the concentration of P and K in leaf, stem and root tissues of watermelon seedlings [37]. Vanadium concentration higher than 47.4 mg L⁻¹ suppressed the accumulation of elements and attenuated solution to shoot translocation of most of the essential elements like Ca, K and Mg in *Setaria viridis* [17]. An overdose of phosphate fertilizers caused vanadium accumulation in rice roots [21]. Due to structural analogy between vanadate and phosphate ions,

the accumulation of vanadium reduces the phosphate which plays a very important physiological role in plants. This may also inhibit the protein phosphatases or bind with different molecules such as ADP/NAD to form ADPV and NADV respectively. Not only that, consumption of such vanadium-contaminated plants by mammals including cattle would ultimately lead to the replacement of phosphate in bones, as well as react with phosphate and sugar alcohol groups of nucleotides to form complexes that inhibit or stimulate the activity of many DNA or RNA enzymes [46].

Chromosome aberrations

Lens culinaris, on exposure to vanadium stress, showed several abnormalities like chromosome breaking, chromosome dispersion, bridge chromosome, chromosome adherence, and ring chromosome on meristematic cells. The chromosomes showed polymorphic inversions by recombination of the breakpoints containing large insertions by transposable elements. Several chromosomal rearrangements and polyploidy took place in lentil mitotic cells in terms of chromosomal changes. The exposed metal caused formation of ligands with proteins which can prevent the persistence of metal ions in DNA protein cross-links that are involved in DNA formation process (inversions, translocations, centric split and fusion, duplications and deletions). Another study demonstrated that vanadium pollution of industrial red mud was responsible for noticeable chromosomal damages in pollen assembly and root cells of food crops [47]. The higher vanadium concentrations inhibited the cell division process significantly [48]. Vanadium stress altered DNA integrity and caused progressive DNA fragmentation in a dose-dependent manner, becoming more significant at 120 mg L⁻¹ in the sensitive genotype of chickpea seedlings [20]. Induction of chromosome aberration was also reported in vanadium-treated onion (*Allium cepa*) root cells, and genotoxic effect was correlated with metal accumulation [49].

Interference with metabolic processes

Singh and Wort (1969) [38] observed that vanadyl sulfate application to sugar beet plants lowered the rate of respiration, decreased the rate of nitrate reductase, glutamic-pyruvic transaminase, phosphatase and invertase activity. On the other hand, CO₂ fixation rate, sucrose synthesis, and activities of the enzymes like sucrose synthetase, sucrose phosphate synthetase and uridine diphosphate glucose-pyrophosphorylase were stimulated. Vanadium causes disability of plants for nutrient absorption, which is the outcome of H⁺-ion obstruction which is key part of ATPase translocation in plants. Vanadium is one of the most potent known inhibitors of Na⁺/K⁺ ATPase, which strongly hydrolyzes at ATP site. It also extensively inhibits working ability of the plasma membrane hydrogen-translocation ATPase [50], which help plants to uptake nutrients by the cells. Moreover, vanadium increased the activity of ATP-dependent GSH-conjugated transport, and ATP Binding Cassette (ABC) transporter, while highly reduced the activity of divalent cation transporter, Drug Metabolite Transporter (DMT) and Zinc-Iron Permease (ZIP) [19].

Conclusion and Future Perspectives

Although vanadium at lower concentration plays some positive roles in plants, gradually increasing concentration of vanadium in soil and water bodies are largely related to negative effects on growth and development, mineral nutrition, plant-water relations, cellular and membrane integrity, enzymatic machinery, photosynthesis and grain yield due to vanadium uptake and bioaccumulation beyond

the threshold limit. Oxidative damages are triggered leading to the generation of ROS, which damages the biomacromolecules like DNA, proteins and lipids. Future studies should be focused on more precise understanding of the translocation, accumulation and partitioning of vanadium in a concentration-dependent manner in different plant tissues as well as different stages of plant growth. The threshold limit of vanadium for individual plant and particularly crop species should be determined to elucidate the tolerance and homeostasis mechanism. This will also help us to design phytoremediation strategies for reclamation of vanadium-contaminated sites in an eco-friendly manner. Moreover, the mechanism of vanadium-induced tolerance should be adequately explored at the genomic, proteomic and molecular levels to develop transgenic plants capable of tolerating high vanadium concentration and produce sufficient yield.

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