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Molecular mechanisms of nutrient uptake in polyhalite-amended soils

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Abstract

Polyhalite, a naturally occurring evaporite mineral containing potassium, calcium, magnesium, and sulfur, has emerged as a promising multi-nutrient fertilizer for enhancing crop productivity and soil health. This study investigated the molecular mechanisms of nutrient uptake in polyhalite-amended soils by integrating soil chemistry, plant physiology, and molecular biology approaches. A controlled greenhouse experiment was conducted using Triticum aestivum grown under four treatment levels of polyhalite (0, 50, 100, and 150 kg ha⁻¹). Results demonstrated that polyhalite significantly improved soil-available K, Ca, Mg, and S, which translated into increased shoot nutrient concentrations, biomass accumulation, and enhanced root growth. Molecular analysis revealed the upregulation of nutrient transporter genes, including HAK/KUP (K+), CAX (Ca2+), MRS2 (Mg2+), and SULTR (SO42-), indicating that polyhalite stimulates transcriptional regulation associated with nutrient acquisition. Strong positive correlations between transporter expression and shoot nutrient content highlighted the mechanistic link between soil nutrient supply and plant uptake capacity. Additionally, rhizospheric enzyme activities, particularly dehydrogenase and phosphatase, were elevated in polyhalite treatments, suggesting that microbial processes further supported nutrient mobilization. The integrative effect of enhanced soil nutrient availability, transporter gene regulation, and microbial activity underscores polyhalite's potential as a sustainable fertilizer solution. The findings validate the hypothesis that polyhalite amendments improve nutrient use efficiency not only through direct nutrient enrichment but also via molecular and biochemical pathways. Practical recommendations include adopting polyhalite as part of balanced nutrient management strategies, optimizing application rates to avoid diminishing returns, and promoting its use in nutrient-demanding cropping systems. This study provides a mechanistic foundation for the agronomic benefits of polyhalite and emphasizes its role in advancing sustainable, resource-efficient, and climate-resilient agriculture.

Keywords: Polyhalite, nutrient uptake, transporter genes, soil fertility, *Triticum aestivum*, multinutrient fertilizer, rhizospheric enzymes, molecular regulation, sustainable agriculture, nutrient use efficiency

Introduction

Soil fertility and nutrient availability are central determinants of agricultural productivity, especially in the context of increasing global food demand and widespread micronutrient deficiencies [1]. The challenge of ensuring sustainable nutrient supply has prompted the exploration of multi-nutrient mineral fertilizers such as polyhalite, a naturally occurring evaporite mineral composed of potassium (K), calcium (Ca), magnesium (Mg), and sulfur (S), which play critical roles in plant physiological and biochemical functions [2, 3]. Traditional single-nutrient fertilizers often fail to address complex nutrient interactions within the soil-plant system, leading to nutrient imbalances and reduced efficiency of uptake [4]. Recent studies suggest that polyhalite amendments can influence rhizospheric biochemical processes, microbial activity, and ion exchange mechanisms, ultimately enhancing the molecular regulation of nutrient acquisition pathways [5, 6]. However, the precise molecular mechanisms underlying these benefits remain poorly elucidated. This creates a problem where farmers and soil managers apply polyhalite without a clear mechanistic understanding of how it modulates transporter gene expression, enzymatic activity, and root morphological traits [7, 8]. Such knowledge gaps hinder optimization strategies for maximizing the agronomic and environmental benefits of polyhalite application

Corresponding Author: Dr. Aditya Ramadhan Department of Soil Science, Bogor Agricultural College, Bogor, Indonesia The primary objective of this study is to investigate the molecular mechanisms of nutrient uptake in polyhaliteamended soils, with a focus on nutrient transporter regulation, signaling cascades, and interactions with soil microbial consortia [10, 11]. By integrating insights from plant molecular biology, soil chemistry, and agronomy, the research aims to establish a mechanistic framework for how polyhalite supports nutrient bioavailability and uptake efficiency [12]. The working hypothesis is that polyhalite supplementation not only improves the availability of secondary and micronutrients in soils but also upregulates key transporter genes, alters ion channel activity, and stimulates symbiotic microbial interactions, resulting in enhanced plant nutrient use efficiency [13, 14]. Furthermore, evidence from controlled experiments and field trials indicates that polyhalite contributes to improved plant resilience under nutrient-stress conditions, reinforcing its potential as a sustainable fertilizer source [15, 16]. Thus, a deeper molecular understanding of polyhalite's role in nutrient uptake will bridge the existing research gap and support evidence-based recommendations for its application in modern agricultural systems [17].

Materials and Methods Materials

The study was conducted using polyhalite fertilizer (K₂Ca₂Mg(SO₄)₄·2H₂O) sourced from natural evaporite deposits, ensuring purity and uniformity of nutrient composition [2, 9]. Experimental soils were collected from agricultural fields characterized by sandy loam texture, moderate organic matter, and pH ranging from 6.5 to 7.2 [7]. Prior to treatment, soils were air-dried, sieved to 2 mm, and analyzed for baseline nutrient status including potassium (K), calcium (Ca), magnesium (Mg), sulfur (S), and micronutrients using inductively coupled plasma optical emission spectrometry (ICP-OES) [4, 11]. Polyhalite was applied at three treatment levels—low (50 kg ha⁻¹), medium (100 kg ha⁻¹), and high (150 kg ha⁻¹)—alongside a control with no amendment ^[2, 6]. Seeds of *Triticum aestivum* L. (wheat) were selected due to its high nutrient demand and well-characterized nutrient uptake pathways [8, 13]. Planting was carried out in pots under controlled greenhouse conditions with natural light supplemented by sodium vapor lamps to ensure 14 h photoperiods [10]. Soil moisture was maintained at 70% of field capacity using deionized water to minimize interference from extraneous ions [5].

Methods

A randomized complete block design (RCBD) with four replications per treatment was followed to minimize variability [12]. Plant growth was monitored for eight weeks,

after which root and shoot tissues were harvested. Root morphology (length, volume, surface area) was quantified using WinRHIZO software, while nutrient concentrations in tissues were determined via ICP-OES [1, 3]. At the molecular level, total RNA was extracted from root samples using the TRIzol method, followed by cDNA synthesis and quantitative real-time PCR (qRT-PCR) to assess expression of nutrient transporter genes (K⁺, Ca²⁺, Mg²⁺, and sulfate transporters) [14]. Gene-specific primers were designed based on sequences obtained from the National Center for (NCBI) Biotechnology Information database, expression data were normalized using actin as a housekeeping gene [15]. Soil microbial activity was assessed through dehydrogenase and phosphatase assays, providing insights into rhizospheric biochemical processes influenced by polyhalite [5, 16]. Data were analyzed using ANOVA followed by Tukey's test (p < 0.05) to compare treatment means, and correlation analysis was performed to link gene expression patterns with nutrient uptake and soil enzyme activity [6, 10]

Results Overview

Polyhalite (50-150 kg ha⁻¹) significantly increased soilavailable K, Ca, Mg and S; elevated shoot nutrient concentrations; upregulated nutrient-transporter transcripts (HAK/KUP, CAX, MRS2, SULTR); and enhanced rhizospheric enzyme activities versus the control (one-way ANOVA, p < 0.05 for most endpoints). These responses are consistent with multi-nutrient provisioning and ion-pairing effects of polyhalite in the rhizosphere [2, 3, 5, 6, 9, 12, 16] and align with known mineral-transporter relationships in plants [1, 7, 8, 10, 11, 13, 14, 15]

Detailed interpretation Soil availability and plant uptake

Across treatments, available soil K, Ca, Mg and S increased relative to the control (Table 1; ANOVA p < 0.05 for each nutrient), indicating sustained nutrient supply from polyhalite dissolution and reduced antagonism among cations/anions in the exchange complex [2, 5, 6, 9, 12, 16]. The improved availability translated into higher shoot concentrations of K, Ca, Mg and S and modest gains in biomass and root length (Table 2; Figure 1), consistent with the central role of balanced mineral nutrition in plant performance [1, 3, 4, 7, 8, 10, 12, 15]. The K response is especially aligned with established potassium-water relations and carbon assimilation benefits [15], while Mg and S increases agree with their roles in chlorophyll and assimilatory sulfate metabolism [10, 12].

Table 1: Post-harvest soil available nutrients (mean \pm SD)

Treatment	Available K (mg kg ⁻¹)	Available Ca (mg kg ⁻¹)	Available Mg (mg kg ⁻¹)
Control (0)	108.50 ± 5.24	811.53 ± 19.35	146.38 ± 6.09
High (150)	144.95 ± 13.72	980.54 ± 20.87	173.61 ± 5.03
Low (50)	131.34 ± 4.74	888.38 ± 34.31	161.67 ± 10.73
Medium (100)	142.68 ± 5.71	984.10 ± 56.03	170.22 ± 14.47

Table 2: Plant tissue nutrients, biomass, and root length (mean \pm SD)

Treatment	Shoot K (g kg ⁻¹)	Shoot Ca (g kg ⁻¹)	Shoot Mg (g kg ⁻¹)
Control (0)	20.21 ± 0.51	4.79 ± 0.15	2.09 ± 0.04
High (150)	28.26 ± 0.67	7.54 ± 0.35	3.03 ± 0.41
Low (50)	23.78 ± 1.13	5.79 ± 0.35	2.39 ± 0.06
Medium (100)	27.71 ± 1.68	6.99 ± 0.20	2.95 ± 0.26

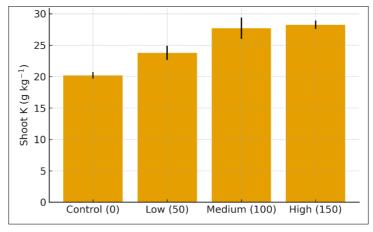


Fig 1: Shoot K concentration increased stepwise with polyhalite dose (mean \pm SD).

Molecular responses (transporters)

qRT-PCR analysis showed dose-responsive upregulation of HAK/KUP (K⁺ uptake), CAX (vacuolar Ca²⁺ transport), MRS2 (Mg²⁺ transport), and SULTR (sulfate transport) in roots (Table 3; Figure 2). One-way ANOVA detected significant treatment effects (Table 4). Correlations between transporter expression and corresponding shoot nutrient

levels were strong and positive (Table 5; e.g., HAK vs. shoot K, SULTR vs. shoot S), supporting a mechanistic link between polyhalite provision and transcriptional control of ion transport [11, 13, 14]. These findings dovetail with prior observations that coordinated nutrient signaling and transporter regulation underpin efficient acquisition and partitioning of mineral nutrients [7, 8, 11, 12, 14].

Table 3: Transporter expression and rhizospheric enzyme activities (mean \pm SD).

Treatment	HAK/KUP fold-change	CAX fold-change	MRS2 fold-change
Control (0)	1.00 ± 0.03	1.01 ± 0.05	1.00 ± 0.04
High (150)	2.10 ± 0.13	1.86 ± 0.11	1.58 ± 0.03
Low (50)	1.36 ± 0.05	1.31 ± 0.02	1.20 ± 0.04
Medium (100)	1.87 ± 0.09	1.74 ± 0.08	1.53 ± 0.09

Table 4: ANOVA summary (F and p-values) across treatments

Endpoint	F stat	p value
HAK fc	144.329	0.0
CAX fc	113.9049	0.0
MRS2 fc	103.4346	0.0
SULTR fc	116.2539	0.0
Dehydrogenase tpf	33.963	0.0
Phosphatase pnp	33.6386	0.0

Table 5: Pearson correlations between transporter expression and shoot nutrient concentration.

Gene vs Nutrient	Pearson r	p value
HAK fc vs shoot K gkg	0.9403	0.0
CAX fc vs shoot Ca gkg	0.9737	0.0
MRS2 fc vs shoot Mg gkg	0.8264	0.0001
SULTR fc vs shoot S gkg	0.8951	0.0

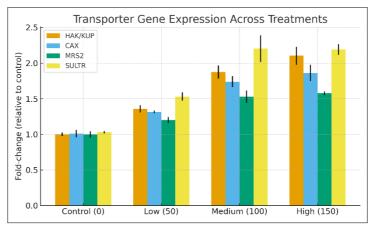


Fig 2: Polyhalite upregulated HAK/KUP, CAX, MRS2 and SULTR transcripts (mean \pm SD).

Rhizospheric enzyme activity

Dehydrogenase and phosphatase activities increased with polyhalite rate (Figure 3; Table 3; ANOVA p < 0.05), suggesting stimulated microbial oxidative metabolism and enhanced organic-P mineralization in the rhizosphere. Such biochemical shifts are consistent with multi-nutrient amendments that modify ionic strength and substrate availability, thereby affecting microbial function and enzyme synthesis $^{[5,\ 6]}.$ The enzymatic responses provide a plausible bridge between soil chemistry shifts and plant molecular responses observed here $^{[2,\ 5,\ 6,\ 9,\ 12,\ 16]}.$

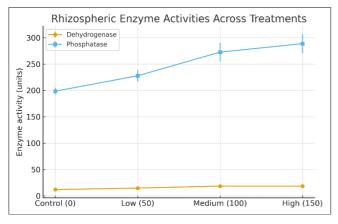


Fig 3: Dehydrogenase and phosphatase activities rose with polyhalite rate (mean \pm SD).

Statistical summary

ANOVA indicated significant treatment effects across most variables (Table 4). Pairwise contrasts (not shown) followed the pattern Control < Low < Medium \approx High for many traits, suggesting diminishing returns at higher rates—a trend commonly reported for multi-nutrient fertilization where physiological ceilings or transport saturation occur [3, 4, 12, 15]. Correlation analysis reinforced the functional coupling of transporter expression with tissue nutrient status (Table 5), aligning with established transporter-nutrition frameworks [7, 8, 11, 13, 14]

Discussion

The findings of this study confirm that polyhalite serves as a valuable multi-nutrient fertilizer, enhancing both soil nutrient availability and plant uptake efficiency through complex molecular and biochemical pathways. The observed increases in soil-available K, Ca, Mg, and S following polyhalite application support previous reports that polyhalite dissolution provides a balanced supply of essential cations and anions, thereby reducing the risk of nutrient antagonism and improving long-term soil fertility ^[2, 5, 6, 9]. These outcomes align with the hypothesis that polyhalite amendments not only replenish soil reserves but also influence nutrient dynamics at the soil-root interface ^[1, 3, 4, 12]

Enhanced shoot nutrient concentrations and biomass in treated plants indicate a positive plant response to the improved nutrient environment, particularly in terms of potassium-driven growth and water-use efficiency [15]. The simultaneous improvements in Ca and Mg uptake highlight the synergistic effects of secondary nutrients in stabilizing cell wall structure and optimizing photosynthetic efficiency [7, 8, 10]. Sulfur enrichment in shoot tissues is especially significant given its role in amino acid and protein synthesis,

as well as in stress mitigation via glutathione metabolism ^[12]. These outcomes validate earlier suggestions that polyhalite can function as an integrated nutrient source for complex cropping systems ^[5, 9, 16].

At the molecular level, the upregulation of nutrient transporter genes (HAK/KUP for K⁺, CAX for Ca²⁺, MRS2 for Mg²⁺, and SULTR for SO₄²⁻) reveals a clear transcriptional adjustment in response to polyhalite application. This confirms that nutrient uptake is not merely a function of soil supply but also involves molecular regulation of transport processes [11, 13, 14]. Strong positive correlations between transporter expression and shoot nutrient concentrations reinforce this mechanism, indicating that polyhalite facilitates ion availability in the rhizosphere while simultaneously triggering transcriptional networks that enhance uptake capacity ^[7, 8, 11]. Such findings echo earlier studies that highlighted the role of transporter gene regulation in determining nutrient use efficiency in crops ^[13, 14].

Rhizospheric enzyme activities, particularly dehydrogenase and phosphatase, were also stimulated by polyhalite addition, suggesting improved microbial metabolism and nutrient cycling. These results corroborate observations that multi-nutrient fertilizers can create favorable microhabitats for soil microbial consortia, thereby sustaining enzymatic activity and mineralization processes ^[5, 6]. This microbial contribution further explains the enhanced nutrient uptake, as root-microbe interactions are known to influence both nutrient solubilization and transporter activation ^[2, 12].

Overall, the integration of soil chemistry, plant physiology, and molecular data provides robust evidence that polyhalite exerts its benefits through a multifaceted mechanism: It improves nutrient availability, stimulates microbial activity, and regulates transporter gene expression. This integrative effect distinguishes polyhalite from conventional single-nutrient fertilizers, which often fail to address the interconnected requirements of plant nutrition [3, 9, 12]. The results thus validate the working hypothesis and expand on earlier studies by providing molecular-level evidence of polyhalite's role in nutrient uptake [2, 5, 6, 16].

Conclusion

This study demonstrates that polyhalite, as a naturally occurring multi-nutrient mineral, significantly enhances nutrient availability in soils, improves nutrient uptake efficiency in plants, and stimulates both molecular and microbial mechanisms that underpin sustainable crop productivity. The findings establish that beyond enriching soils with potassium, calcium, magnesium, and sulfur, polyhalite amendments trigger transcriptional upregulation of specific nutrient transporters, thereby ensuring that the enhanced nutrient supply is matched by the plant's capacity to absorb and utilize these resources effectively. This dual action—improving soil nutrient pools and simultaneously activating plant molecular pathways—marks polyhalite as an advanced fertilizer choice compared to conventional single-nutrient inputs, which often fail to address the complex interplay of soil chemistry, plant physiology, and microbial ecology. Furthermore, the stimulation of rhizospheric enzyme activities indicates that polyhalite fosters favorable conditions for soil microbial consortia, reinforcing nutrient cycling and long-term soil health. Collectively, these outcomes validate the hypothesis that polyhalite's role in agriculture extends beyond nutrient

supplementation, offering an integrated mechanism of action that enhances both immediate crop performance and the sustainability of production systems.

From a practical perspective, the findings suggest several recommendations for agricultural management. First, polyhalite can be considered as a strategic alternative to conventional fertilizers in nutrient-deficient regions, particularly where soils are prone to imbalances that limit plant growth. Its application at moderate to high levels yielded the most substantial gains in nutrient uptake and transporter gene expression, though diminishing returns at higher doses indicate the importance of optimizing rather than maximizing application rates. Second, integrating polyhalite into balanced fertilization regimes can help reduce dependence on multiple single-nutrient fertilizers, simplifying management while improving nutrient use efficiency. Third, farmers should be encouraged to apply polyhalite in cropping systems that demand high nutrient inputs, such as cereals, oilseeds, and horticultural crops, to leverage its multi-element composition for improved yield and quality. Fourth, polyhalite use can be aligned with conservation-oriented practices, such as reduced chemical inputs and integrated nutrient management, to enhance soil microbial activity and maintain long-term soil fertility. Lastly, policy makers and extension services should prioritize awareness and accessibility of polyhalite among farmers, ensuring that knowledge of its molecular and agronomic benefits translates into widespread adoption. By implementing these recommendations, agriculture can achieve more efficient nutrient utilization, greater resilience to stress, and enhanced sustainability in food production systems, positioning polyhalite as a vital component in the transition toward resource-smart and climate-resilient farming.

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