Responses of mineral nutrient contents and transport in red clover under aluminum stress

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Abstract
Aluminum toxicity is considered the main factor underlying nutrient deficiencies and growth limitations of plants in acidic soil. Red clover (Trifolium pratense L.) is an important legume grass distributed worldwide, and it has medicinal value and strong adaptability to acidic soil with Al. However, few studies have focused on the relationship between nutrient uptake and Al stress. In this study, the changes in nutrients in the organs (root, stem, and leaf) of the cultivars Brilliant, Dory, and Haifa under high aluminum stress were detected. The results indicated that the contents of macronutrients and micronutrients were significantly influenced by Al3+ concentrations and the interaction between Al3+ concentrations and cultivars (P < 0.05). Under the Al3+ treatments, the contents of phosphorus (P) and magnesium (Mg) significantly decreased by 30.5% to 87.2% and 6.3% to 39.2%, respectively. However, potassium (K), zinc (Zn), and manganese (Mn) increased significantly, and these changes were closely correlated with Al resistance. The effect of Al stress on the copper (Cu) content varied with the plant organs, with Cu reduced in the roots but increased in the stems and leaves. Furthermore, the change ranges of nutrition contents in the sensitive cultivar were largest except for Cu. For example, the contents of Ca dropped by 26% in Brilliant leaves but decreased by less than 4% in the leaves of Haifa and Dory at 5-mM Al3+. Moreover, the nutrient transport efficiencies were positively correlated with the Al3+ treatment concentrations in resistant cultivar except for Mg.

KEYWORDS
acidic soil, aluminum stress, nutrient uptake, red clover

1 | INTRODUCTION

Acidic soil is widely distributed in tropical and subtropical areas of the world and accounts for approximately 30% of the total area and 50% of the arable land in the world (Sade et al., 2016; Senger et al., 2014). Due to climate- and human-related factors, such as industrial emissions, unreasonable land use, and acid rain, the area of acidic soils is still expanding annually (Bojórquez et al., 2017). The normal growth of plants is limited by acidic soil, which causes yield losses between 25% and 80% depending on the crop species (Sade et al., 2016). Thus, soil acidification must be mitigated and resolved for further soil utilization.

Al stress is considered a serious limiting factor for acidic soils. At pH < 5.5, Al is easily converted to ions that can be absorbed by
plants and then severely inhibit their growth and development (Matsumoto, 2000). Therefore, Al-tolerant plants must be cultivated to improve crop production (Senger et al., 2014).

Nutrients are essential for plant growth. Al toxicity is associated with severe changes in the root system, which consequently interferes with nutrients uptake, transport, and utilization (Rahman et al., 2018). Al toxicity usually leads to a reduction in the uptake of many nutrients in most plants, such as P, Ca, Mg, K, Zn, and Mn (Macêdo & Jan, 2008; Ribeiro et al., 2013) and inhibits the development of these plants. Nevertheless, the ability to increase the concentrations of macronutrients and micronutrients in the roots and stems is considered to be directly related to Al resistance when Al is present in the soil (Bojórquez et al., 2017; Foy, 1988).

Red clover is a major forage legume cultivated over approximately 4 million ha of land worldwide as an animal feed and to improve agricultural system soils (Riday, 2010; Sindic & Riday, 2020). Red clover can adapt well to acidic, aluminous, and poor-quality soils (Baligar et al., 1987). The adaptation mechanism of red clover to Al stress from the perspective of plant nutrition.

Al was thought to induce an increase in the P, K, Mg, Mn, and Zn contents in shoots of red clover, whereas the concentrations of Fe and Cu decreased at less than 100 μmol/L (Baligar et al., 2001). However, few reports have focused on the mechanism of nutritional absorption of red clover to Al toxicity. To explore the relationship between the nutrient contents and Al resistance, three cultivars of red clover were treated with high concentrations of Al(III) (from 1 to 5 mM) for 30 days, and the contents of nutrition in the leaves, stems, and roots were detected. The study results were useful for explaining the adaptation mechanism of red clover to Al stress from the perspective of plant nutrition.

### 2 | MATERIALS AND METHODS

#### 2.1 | Experimental design

The seeds of Brilliant (Al sensitive) and Haifa and Dory (Al resistant), which were purchased from the Lanzhou seed market, were disinfected with 2% sodium hypochlorite solution for 10 min and thoroughly rinsed with distilled water. Then, these disinfected seeds were dried and spread evenly in dishes containing quartz sand. At 10 days old, plantlets were transferred to a basket and fixed on vermiculite, which was placed in a basin containing 300 ml of nutrition solution composed of the following micronutrients: KNO$_3$ (2.5 mM), Ca(NO$_3$)$_2$·4H$_2$O (2.5 mM), MgSO$_4$·7H$_2$O (1 mM) and (NH$_4$)$_4$H$_2$PO$_4$ (0.5 mM), NaFeEDTA (50 μM), H$_2$BO$_3$ (7.5 μM), MnCl$_2$ (1.25 μM), CuSO$_4$ (0.5 μM), ZnSO$_4$ (1 μM) and (NH$_4$)$_6$Mo$_7$O$_24$·4H$_2$O (2.5 μM). The pH was adjusted to 4.5 with HCl and checked three times a week. Every week, the solutions were renewed, and the tanks were randomly rearranged. After cultivating for 50 days, the plants were treated with the nutrition solution with different concentrations of AlCl$_3$ (0, 1, 3, and 5 mM). Each treatment sets six replicates. The experiment was conducted in a greenhouse at 30/25°C day/night temperature. The day lengths were natural from April to June. After 30 days, all plants per treatment were harvested.

#### 2.2 | Nutrition content measurements

Roots were rinsed for 1 min with SrCl$_2$ (1 mM) to remove ions from the free space. Leaves, stems, and roots were separately collected and oven-dried at 65°C for 48 h. Plant samples (0.25 g) were digested in a 10-ml mixture of HNO$_3$, H$_2$SO$_4$, and HClO$_4$ (volume ratio 8:1:1). The phosphorus content was determined using molybdenum antimony colorimetry. Flame spectrophotometry was then used to determine the potassium and calcium contents, whereas flame atomic absorption spectrometry was then used to determine Mg, Fe, Cu, Zn, and Mn (Chu et al., 2013). The results were expressed in mg/g of dry weight.

#### 2.3 | Statistical analysis

The rate of ion transport (RI) from the root to leaf is one of the indicators that indicates the transfer of elements from the root to the leaf, which was calculated using the following equation:

$$ RI = \frac{IL}{IR}, $$

where IL and IR are the amounts of ions in the leaves and roots, respectively.

The rate of decrease (increase) indicates the degree of decrease (increase) of nutrients under treatment compared with the control. Values are given as the mean ± standard deviation from at least six independent replicate deviations as calculated from data from independent experiences. A comparison between Al(III) exposure periods and the control and comparison between genotypes was performed using a one-way analysis of variance (ANOVA), followed by Duncan’s procedure (P < 0.05). For this statistical analysis, the software package SigmaStat was used (SPSS 20.0). Correlations between the Al(III) concentrations and the species and nutrition contents were tested by two-way ANOVA tests.

### 3 | RESULT

#### 3.1 | Macronutrients

The macronutrient contents of the red clover organs (root, stem, and leaf) were markedly affected by Al(III) (Figure 1–4). With increasing Al(III) concentrations, the contents of P and Mg decreased while the contents of K increased. Significant decreases in Ca were only observed in the roots. Two-way ANOVA tests indicated that the contents of macronutrients (P, K, and Ca) were significantly affected by the Al(III) concentrations (A) and their interactions with the Al(III) concentration...
and cultivar (A*C) \( (P < 0.05) \), whereas the content of Mg was not affected (Table 1).

The contents of P in the organs of the three cultivars significantly dropped with increasing Al\(^{3+}\) concentration \( (P < 0.05) \) (Figure 1a–c). The contents of P dropped by approximately 50% in the stems and roots at 1-mM Al\(^{3+}\), whereas those in the leaves decreased by more than 30%. The reduced ranges of stems were highest among the three organs of the three cultivars, and the opposite was true in the leaves, which was the lowest. In the 5-mM Al\(^{3+}\) treatments, the contents of P in the roots, stems, and leaves of Haifa decreased by 79.1%, 85.8%, and 57.2%, respectively. The most obvious reduction was shown in the sensitive cultivar Brilliant (Figure 1a–c). For example, the content of P was reduced by 37.9% at 5-mM Al in the leaves of Brilliant but by less than 30% in the other two cultivars. The transportation of P from the roots to leaves significantly increased in Haifa and Dory (Table 2).

The K content increased with increasing Al\(^{3+}\) concentration from 0 to 5 mM in the organs of the three cultivars (Figure 1d–f). The contents of K in the leaves of the three cultivars, which were highest among three organs, increased more obviously than those in the roots, which were lowest among three organs. The content of K in the roots of Haifa was 18.7 mg/g at 5-mM Al\(^{3+}\), whereas it was 23.1 mg/g in the roots. The increase of K in the leaves of Haifa was 12.8% at 5-mM Al\(^{3+}\) but 20.8% in the roots.

However, the lowest increases were observed in the roots of the resistant cultivars among the three cultivar roots. At 5 mM, the contents of K in the Brilliant, Dory, and Haifa roots significantly increased by 37.7%, 34.6%, and 12.9% \( (P < 0.05) \), respectively. However, the translocation of K significantly increased in Haifa but significantly decreased in the other cultivars \( (P < 0.05) \) (Table 2).

Al toxicity induces a transient rise in cytosolic Ca, which results in an increase in callose synthesis, impedes the transport of auxin, and inhibits the absorption of Ca (Sade et al., 2016). The contents of Ca showed obvious decreases in the roots and leaves of the three cultivars except for the roots and leaves of Dory at 1 mM, which showed significant increases of 32.4% and 12.5%, respectively \( (P < 0.05) \) (Figure 2a,c). The contents of Ca in the stems of Haifa and Dory were relatively stable and had no

![Figure 1](image)

**FIGURE 1** P and K contents of red clover under Al stress. The lowercases denote significant differences among the different Al\(^{3+}\) concentrations for red clover organs. And the upper cases denote significant differences among three cultivars. The differences in each parameter were tested by one-way analysis of variance (ANOVA) at the \( P < 0.05 \) level. The bars represent the means ± SEs \( (n = 6) \)
significant change. However, the contents of Ca in the stems of Brilliant plants significantly increased (Figure 2b).

The content of Ca was highest in Brilliant, which was the most sensitive among the three cultivars. Compared with the control, Ca decreased by 71.8% in the Brilliant roots at 5 mM and by 65.1% and 49.5% for Dory and Haifa, respectively. Ca decreased between 4.9% and 26% in Brilliant leaves with increasing Al³⁺ concentrations but by less than 3.6% in those of Dory and Haifa. The translocation of Ca from the roots to the leaves obviously increased in the three cultivars in response to Al stress (Table 2). The effects were significant in Brilliant and Dory.

Al stress caused decreases in the Mg contents in the organs of the three cultivars (Figure 2d–f). The Mg decrease in the leaves was the highest at up to 39.2% at 5 mM, whereas that in the roots was less than 10%.

The decrease of the Mg contents in the stems and leaves in the sensitive cultivar Brilliant were largest among the three cultivars. The decreases in the stems were 24.5%, 1.1%, and 8.8% in the Brilliant, Dory, and Haifa cultivars with 5-mM Al³⁺, respectively. Nevertheless, slight decreases in the Mg contents in the roots were observed in the three cultivars, and significant decreases were not observed among the three cultivars. Mg translocation significantly decreased in response to Al stress in the three cultivars, and the effect was more marked in the Brilliant cultivar than in the other cultivars (Table 2).

These results indicated that the decreases in macronutrient contents were correlated with the capacity of Al resistance. Among the three cultivars, Brilliant was the most sensitive in terms of changes in macronutrient contents, followed by Dory and Haifa.

### 3.2 | Micronutrients

Al stress had marked effects on the micronutrient contents of red clover, although the micronutrient contents were more stable than the macronutrient contents with the Al³⁺ treatments (P < 0.05) (Figures 3 and 4). The two-way ANOVA tests indicated that the contents of micronutrients (Ca, Zn, and Mn) were significantly affected by the Al³⁺
concentrations (A) \((P < 0.05)\). Moreover, the contents of Zn and Cu were also affected by the cultivar and their interactions (Table 1).

The two-way ANOVA tests indicated that the contents of Mn and Zn were significantly positively affected by the \(\text{Al}^{3+}\) concentration and the interactions between the \(\text{Al}^{3+}\) concentration and cultivar (Table 1). However, Al stress had no significant effect on the translocation of Mn and Zn (Table 2). In addition, the Zn contents of the Haifa organs did not show significant changes with increasing levels of Al.

With increasing \(\text{Al}^{3+}\) concentration, the contents of Zn in the organs of the three cultivars showed an increasing trend (Figure 3a–c). The increases in Zn contents in the leaves and roots of Dory were most obvious among the three cultivars, which were more than 45% at 5 mM and less than 30% in other cultivars. The contents of Zn in the stems of the three cultivars showed stable increases by no more than 5%, and the rate of increase was lowest among the three organs.

The contents of Mn increased obviously, although significant changes were not observed at 1- and 3-mM \(\text{Al}^{3+}\) (Figure 3d–f). The rate of increase of the Mn contents in Brilliant were largest among the three cultivars. At 5 mM, the contents of Mn in the roots, stems, and leaves of Brilliant significantly increased by 11.6%, 11.2%, and 14.5%, respectively, whereas those in other cultivars were less than 10%. Moreover, the contents of Mn in the Haifa roots increased by 4.3% at 5 mM, which was the lowest.

The effect of \(\text{Al}^{3+}\) on the Cu content varied with plant organs when subjected to Al treatments. The contents of Cu in the roots dropped by up to 83.4% (Figure 4a), whereas those in the stems and leaves stably increased by less than 28% (Figure 4b,c). The rate of change in the roots was largest.

The contents of Cu in the resistant cultivar Haifa roots were most sensitive to \(\text{Al}^{3+}\) among the three cultivars, whereas the rate of decrease in Brilliant was the lowest. The Cu content significantly decreased by more than 80% in Haifa roots at 3- and 5-mM \(\text{Al}^{3+}\). At 3-mM \(\text{Al}^{3+}\), the Cu content decreased by 11.2%, 51.2%, and 83.3% in Brilliant, Dory, and Haifa roots, respectively. However, a significant decrease in Cu of 60.1% in Brilliant was only observed at 5-mM \(\text{Al}^{3+}\). Interestingly, Cu translocation to the leaves significantly increased only in Haifa under Al stress (Table 2).

**FIGURE 3** Zn and Mn contents of red clover under Al stress. The lowercases denote significant differences among the different \(\text{Al}^{3+}\) concentrations for red clover organs. And the upper cases denote significant differences among three cultivars. The differences in each parameter were tested by one-way analysis of variance (ANOVA) at the \(P < 0.05\) level. The bars represent the means ± SEs \((n = 6)\).
4 | DISCUSSION

Red clover can adapt to acidic and aluminous soils, a wide range of pH values and severe environmental conditions (Baligar et al., 1987). However, changes in plant nutrition are an important condition for determining Al resistance, and greater impacts are observed in Al-sensitive cultivars than in Al-tolerant cultivars for most nutrients (Mariano & Keltjens, 2005; Simon et al., 1994). The macronutrients and micronutrients in red clover were detected under Al stress in the study.

In previous work on red clover, its growth was seriously limited under 200 μM Al³⁺, and the biomass was less than 0.06 g/m⁻² (Baligar et al., 2001). However, red clover can survive under the highest treatment concentration of up to 5-mM Al³⁺ in this study. These differences might be due to the anion inhibition of SO₄²⁻; thus, AlCl₃ might be more suitable for Al toxicity experiments to reduce anion interference.

The results indicated that the contents of K in red clover organs were stimulated under Al stress (Figure 1d–f). Al can limit plant photosynthesis by causing a decrease in stomatal conductance (Akaya &Takenaka, 2001). K participates in regulating stomatal movement and osmotic adjustment; thus, it is an indispensable element in plants (Donega et al., 2013). The increase in K⁺ uptake was counterbalanced by a decrease in the uptake of other cations in rice varieties with different resistances to Al (Jan, 1991). Al³⁺ and K⁺ competed in the K⁺ channel, and a decrease in K uptake was positively correlated with an increase in Al in the root (Giannakoula et al., 2008).

The contents of Zn in red clover also increased under Al stress (Figure 3a–c), which was consistent with results shown in rice, tobacco, and wheat (Clark, 1977; Lin et al., 2015). Zn deficiency often results in the inhibition of growth because Zn protects plants by preventing oxidative damage to DNA, membranes, phosphorus, SH-containing enzymes, chlorophyll, and indole-3-acetic acid (Cakmak, 2000). The level of Zn in rice and tobacco inhibited the generation of O²⁻ and cell death induced by Al³⁺ (Lin et al., 2015). The increase in Zn in red clover may be a response to alleviate the toxicity of Al³⁺.

An obvious increase in the Mn content occurred under the Al treatment. Mn is a micronutrient for preventing free radical damage (Ledig et al., 1991) and could alleviate Al toxicity by inhibiting the uptake of Al³⁺ and reducing oxidative stress (Muhammad et al., 2019). Mn had a positive relationship with the ability of plants to resist Al (Macêdo & Jan, 2008).

The contents of Zn in red clover also increased under Al stress (Figure 3a–c), which was consistent with results shown in rice, tobacco, and wheat (Clark, 1977; Lin et al., 2015). Zn deficiency often results in the inhibition of growth because Zn protects plants by preventing oxidative damage to DNA, membranes, phosphorus, SH-containing enzymes, chlorophyll, and indole-3-acetic acid (Cakmak, 2000). The level of Zn in rice and tobacco inhibited the generation of O²⁻ and cell death induced by Al³⁺ (Lin et al., 2015). The increase in Zn in red clover may be a response to alleviate the toxicity of Al³⁺.

The K, Zn, and Mn contents in the three red clover samples increased significantly, which may be the result of the plant’s ability to inhibit the absorption of Al³⁺ and adapt to acidic aluminum environments in production practice.

Al stress significantly inhibited the uptake of P and Mg in red clover. Compared with other elements, the contents of P in red clover

![FIGURE 4 Cu contents of red clover under Al stress. The lowercases denote significant differences among the different Al³⁺ concentrations for red clover organs. And the upper cases denote significant differences among three cultivars. The differences in each parameter were tested by one-way analysis of variance (ANOVA) at the P < 0.05 level. The bars represent the means ± SEs (n = 6)](image)

| Table 1 | Two-way analysis of variance (ANOVA) of the effects of Al³⁺ concentrations (A), cultivars (C), and their interactions (A*C) on the nutrition contents of red clover |
|---------|----------------------------------|
|         | A     | C       | A*C    |
| P       | −0.785** | −0.004  | −0.751** |
| K       | 0.683** | −0.165  | 0.636** |
| Ca      | −0.328** | 0.215*  | −0.214* |
| Mg      | −0.035  | 0.125   | 0.018   |
| Cu      | −0.308** | −0.288**| −0.437**|
| Zn      | 0.253** | −0.315**| 0.355** |
| Mn      | 0.262** | −0.186  | 0.265** |

Note: The data represent F values at the 0.05 level. *Significance at P < 0.05. **Significance at P < 0.01.
were the most strongly decreased by up to 80% (Figure 1a–c). P deficiency is an important characteristic of aluminum toxicity (Liao, 2006). The complexation between free aluminum and phosphoric acid affects the availability of P, thus inhibiting root absorption and P metabolism in plants (Zhi & Hong, 2016). The decreases in P contents were more pronounced in the sensitive red clover cultivar, and its contents were significantly lower than those in the resistant cultivar (Figure 1a–c). The sensitive cultivar also showed the lowest translocation efficiency of P (Table 2). High concentrations of Al interfered with the uptake of P, and P was also an important nutrient for aluminum tolerance. The contents of P decreased under more than 200-μM Al3+ but increased at less than 100 μM (Baligar et al., 2001). Mg could resist Al by stimulating the secretion of organic acids (Bose et al., 2011). However, the decrease in Mg contents, which was not affected by the Al 3+ concentrations, red clover cultivar or their interactions (Table 2); thus, it was not related to the Al resistance of red clover.

The contents of Ca and Cu in the roots dropped significantly with the Al3+ treatment. Al3+ could block cation transport channels, compete with mineral ions to transport proteins, and inhibit the absorption of cations, which might be the reason for the decrease of Ca and Cu (Sade et al., 2016). Ca has an important effect on the regulation of anion channels and organic acid secretion (Ryan et al., 1997). Al resistance in certain cultivars of wheat, barley, and soybean has been associated with their ability to cope with Al-induced Ca deficiency or limited Ca translocation (Fageria et al., 1988). Apparent increases in Ca translocation from the roots to leaves were observed in this study (Table 2). Efficient transport of Ca constituted a complementary mechanism of Al tolerance for red clover.

Cu is the core element of many oxidases and widely participates in various physiological activities of plants. The increasing Cu contents in the stems and leaves may be useful for alleviating the toxicities of Al3+ in the leaves (Strid, 1996) and might be an important Al-resistant pathway in the resistant cultivar Haifa.

5 | CONCLUSIONS

Different nutritional elements in red clover have different responses to Al3+. The increase in the K, Zn, and Mn contents in the organs of the three cultivars may be due to the resistance of red clover to Al3+. When exposed to aluminum, the contents of P, Ca, Mg, and Mn in the Al-sensitive cultivar of red clover were more obviously affected than those in the Al-resistant cultivar.

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CONFLICT OF INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

AUTHOR CONTRIBUTIONS

Qin Yang: Writing-original draft and review & editing. Yonghe Lin: Investigation and Methodology. Xiaoyan Ren: Data curation. Ling Jin: Writing-review & editing. Chunyan He: Validation. Quan Liu: Writing - review and editing.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ETHICS STATEMENT

This article does not contain in vivo studies with human participants or animals.
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