

Excess aluminum tolerance of the common water-hyacinth (*Eichhornia crassipes*) under greenhouse conditions

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ABSTRACT

Aluminum is a heavy metal toxic to living organisms and is released into soils with a strong acidic composition. The floating aquatic weed *Eichhornia crassipes* (Mart.) Solms is reported as the most widespread invasive vascular plant in the world and is distributed all over Colombia ranging from sea level to the cold Andean highlands. As a consequence of the solubility of Al³⁺ in soils, it flows into fresh water sources where *E. crassipes* grows as an invasive plant. A greenhouse study was conducted in Tunja, Colombia, with the objective of evaluating the growth of aquatic weed in an aqueous substrate with Al³⁺ content similar to those recorded in lakes (0.0, 0.2, 0.4, 0.6, and 0.8 mg L⁻¹ Al³⁺). Biomass production, leaf area, evapotranspiration, water use efficiency, and other allometric variables were evaluated. An increase of 18.2% in the transpiration rate and a reduction between 9.7%-41.8% in the leaf area were found. The latter reduced the value of variables such as the specific leaf area between 9.9%-34.6% and leaf area ratio between 16.7%-40.4%. However, the total dry weight, DM partitioning, root to shoot ratio, leaf weight ratio, and the absolute and relative growth rates did not show significantly different values between treatments. Therefore, Al content found in water sources in Colombia, despite being in the ranges reported as toxic for some aquatic plants, did not significantly affect the growth of *E. crassipes* due to its phenotypic plasticity and anthropic alteration of water sources but rather favor its growth.

Key words: Aquatic weed, evapotranspiration, growth, invasive plant, stress, toxicity.

INTRODUCTION

In Colombia, around 67 million hectares of land have acidity problems which causes increased risk of Al toxicity to all living things, including plants (Casierra-Posada et al., 2008). When soils have a slightly acidic to neutral composition, the naturally occurring Al that is part of the soil would not pose any threat to living things; however, under strongly acidic conditions, this metal is released and is available in solution within the soil, making it toxic (Casierra-Posada and Niño-Medina, 2007). Once in solution within the soil, Al³⁺ can migrate and contaminate water sources. In a study carried out in a Colombian region characterized by strongly acidic soils, a value of 0.14 mg L⁻¹ Al³⁺ was recorded in the water of one of its lakes (Morales Velasco and Salazar Sánchez, 2012). Thus, dissolved Al in freshwater sources represents a risk of toxicity to the biota of rivers and lakes.

Heavy metal toxicity limits plant growth in many environments. Certain metals such as Cu and Zn, are essential micronutrients for plants in low concentrations, but they can become toxic when their concentration exceeds the tolerance levels of plants. On the other hand, metals such as Al and Pb are only known for their toxicity (Hodson, 2012). Although Al is one of the most abundant elements in the earth's crust, it is toxic to many plants when the concentration is greater than 2 to 3 mg kg⁻¹ and soil with a pH of 5.5 (Balsberg Pahlsson, 1990).

In relation to the effect of Al^{3+} in plantlets, it has been found that when seedlings of *Crambe abyssinica* are exposed to Al^{3+} , the damage caused to its development was more severe as the concentration of Al^{3+} increased in the substrate. Thus, as a consequence of exposure to Al^{3+} , decreased growth, biomass accumulation and leafiness, as well as changes observed in DM partitioning in the different organs of the plants were seen (Colodetti et al., 2015). Additionally, it is reported that the presence of Al in the substrate reduces the percentage of germination in seeds of *Triticum aestivum* and *Zea mays*, by 31% and 15%, respectively (Casierra-Posada et al., 2008).

The floating aquatic weed *Eichhornia crassipes* (Mart.) Solms is reported as the most widespread invasive vascular plant in the world and is distributed all over Colombia from sea level to the cold zone (around 3000 m a.s.l.). The plant has a strong impact on the physical-chemical properties of fresh water sources in which it causes alterations in temperature, pH, biological oxygen demand, and nutrient levels. Sometimes it induces a complete decrease in dissolved oxygen in the water which causes the death of a large number of aquatic organisms (Téllez et al., 2008).

Eichhornia crassipes has been seen as a useful or harmful plant in ecosystems. Almeida et al. (2021) mentions that this plant causes serious problems and is therefore necessary to eliminate it from aquatic ecosystems which would have a huge environmental benefit. On the other hand, Ansari et al. (2020) and Sharma et al. (2021) suggest that because the quality of water is frequently altered by various organic and inorganic pollutants, various strategies have been developed to solve this problem. One technique utilizes phytoremediation with aquatic plants such as *E. crassipes* due to their capacity to adapt and tolerate different heavy metals and other types of pollutants. Additionally, the use of cellulose has been taken into consideration as an alternative for the treatment of water sources contaminated with heavy metals. This makes *E. crassipes* very important due to its natural levels of cellulose and its abundance in wetlands, polluted rivers, and lakes (Sayago et al., 2020).

Various studies have been carried out on the management and control of *E. crassipes* and use of its biomass (Ali et al., 2020). However, no studies related to the effect of Al on these plants are reported since studies on the effects of Al^{3+} as a stressor in freshwater macrophytes are particularly scarce, especially when compared with the large number of references available on the effects of this heavy metal on land plants (Gensemer and Playle, 1999). However, it has been mentioned that this invasive plant is very efficient in the elimination of a wide range of metals in water sources, among which is Al, and it is pointed out that this aquatic weed can remove up to 73% of this metal in wastewater from steel effluents (Ali et al., 2020).

A significant correlation has been shown between low pH and high Al^{3+} concentration in acidified fresh water where this metal can reach levels of 0.3 to 1.6 mM (0.008-0.043 mg L⁻¹) and cause a serious metabolic disorder in some hydrophytes (Dickson, 1978; Pettersson et al., 1985). However, it has been shown that in general, aquatic plants can withstand a high degree of pollutants present in sewage leachates without showing obvious signs of a significant reduction in biomass and growth rate (Ali et al., 2020). With this knowledge, the objective of this study was to evaluate the growth of the floating aquatic weed *Eichhornia crassipes*, under aqueous substrate conditions in which Al^{3+} was added in concentrations similar to those found in water sources surrounded by soils with strongly acidic compositions. This allowed its growth to be evaluated under controlled conditions that emulate the conditions that the natural environment offers in order to understand why this weed is such a successful plant in the invasion of water sources.

MATERIALS AND METHODS

The study was carried out in the glass greenhouse of the Universidad Pedagógica y Tecnológica de Colombia (UPTC), in Tunja (5°33'10.62" N, 73°21'23.97" W; 2702 m a.s.l.), Colombia. During the 57 d that this study lasted, the average climatic conditions inside the greenhouse were 16.1 ± 7.8 °C and $72.3 \pm 16.9\%$ relative humidity. Common waterhyacinth plants (*Eichhornia crassipes* (Mart.) Solms, Pontederiaceae) were taken from the La Playa reservoir in Tuta (5°41'14.41" N, 73°15'14.81" W; 2587 m a.s.l.), Colombia. These plants are typically found in the open with an average temperature of 13 ± 6 °C and a relative humidity of $79 \pm 6\%$.

In order to determine information about the growth of the plants at the beginning of the study, 20 out of 170 plants were specifically selected and measured based on their uniformity in terms of their size, leaf area, and total dry weight per plant. The remaining plants were placed in 700 mL containers with a solution containing distilled water and water taken from the La Playa reservoir in a 1:1 ratio. This mixture was used specifically so that the plants grew in an aqueous environment as similar as possible to their place of origin in terms of the microbiota in the water.

Five days after placing them in the containers with the solution, the plants were distributed into five groups of 30 plants each. The containers were then labeled to identify them at the time of inducing excess Al. The criteria for selecting the treatments considered studies such as that of Abdullah (2014), which mentions that the content of Al^{3+} in natural waters is highly variable and dependent on physicochemical and mineralogical factors in the environment. The dissolved Al^{3+} in waters in which the pH is almost neutral usually oscillates between 0.001 and 0.05 mg L^{-1} , but this range can reach values of 0.5-1.0 mg L^{-1} in acidic waters or those rich in organic matter. In cases of extreme acidity such as water sources affected by the acid drainage of mining operations; dissolved Al^{3+} content of up to 90 mg L^{-1} have been recorded. Studies in Colombia such as that by Morales Velasco and Salazar Sánchez (2012), determined the amount of Al^{3+} in lakes in Colombian areas consisting of geologically poorly evolved acidic soils containing a high amount of Al and low amounts of Ca and P. Their study found a pH of 4.63 and an Al^{3+} content of 0.14 mg L^{-1} in the lake water. As a result, the evaluated treatments that would be applied consisted of 0.0 (control), 0.2, 0.4, 0.6, and 0.8 mg L^{-1} Al^{3+} dissolved in water from $\text{Al}(\text{OH})_3 \cdot 7\text{H}_2\text{O}$ (Merck KGaA, Darmstadt, Germany).

Every 3 d the water that was considered evapotranspired was replenished so that the total amount of water was maintained at 700 mL. Finally, with a pH meter (780 pH Meter, Metrohm, Herisau, Switzerland) the pH of the solution was recorded in each of the containers. At the end of the study, 57 d after the start, the plants were removed from their containers and measurements were taken. The leaf area of each plant was determined using an integrated area meter (LI-3000-A, LI-COR, Lincoln, Nebraska, USA). Likewise, dry weight of leaves, petioles, and roots were determined by drying them in oven (UFE 500, Memmert, Schwabach, Germany) at 80 °C until reaching a constant dry weight. With this information, total dry weight per plant, DM partitioning, root to shoot ratio (R/S), leaf area ratio (LAR), specific leaf area (SLA), and leaf weight ratio (LWR) were calculated. Additionally, the absolute and relative growth rate in accordance with the methodology proposed by Hunt (1990) was calculated. The water use efficiency (WUE) was also calculated as the amount of DM as a function of the evapotranspired water per plant.

The plants were placed in the greenhouse using a completely random design with five treatments and 30 replicates per treatment, taking one plant as a replicate. Statistical analysis was performed using the IBM-SPSS version 26.0 application (IBM Corp., Armonk, New York, USA). An ANOVA was performed with Tukey's HSD (honest significant difference) test ($P < 0.05$).

RESULTS AND DISCUSSION

pH of the substrate

At the beginning of the study, without having applied the aluminum hydroxide to the water, an average pH value of 6.68 ± 0.05 was recorded. Since the reagent used to create excess Al was $\text{Al}(\text{OH})_3 \cdot 7\text{H}_2\text{O}$, this caused a slight increase in the pH value of the water in which the plants grew. At the end of the test, the aqueous substrate of the plants in the control treatment had a pH value of 4.46 ± 0.14 . The pH value of the aqueous medium in which the plants treated with 0.2 and 0.4 mg L^{-1} Al^{3+} grew, increased by 0.12 and 0.18 units, respectively, above the average value found for the growth medium in control plants. Similarly, plants treated with 0.6 and 0.8 mg L^{-1} Al^{3+} resulted in an increase in pH by 0.26 and 0.51 units respectively, above the average value of control. Therefore, plants of all treatments grew in a pH range of 4.46 to 4.97, with a standard deviation of ± 0.25 among all treatments.

Rodríguez-Zambrano and Aranguren-Riaño (2014) reported an average pH of 4.93 ± 1.18 for the water in the La Playa reservoir where the plants were obtained for the experiment. As a result, pH of the water from the reservoir of origin of the plantlets and that of the aqueous substrate in which the plants grew in the greenhouse show great similarity. So, growth of plants in this study was not limited by pH, but as a consequence of the effect of Al^{3+} on the plants.

The pH of the medium in which *E. crassipes* plants grow is of great importance for their normal metabolism and therefore for their growth. Téllez et al. (2008) reports that this value should range between 6.0 and 8.0 and added that if the pH value of the medium in which the plants grow is outside this range, the plant will adjust the pH until it reaches a value close to its comfort range. The maximum growth of *E. crassipes*, in terms of number of plants and dry weight, occurs when pH is 7.0. A pH of 3.2 to 4.2 would be very toxic to the plant, while pH from 4.2 to 4.3 and 4.3 to 4.5 would cause an inhibitory and possibly inhibitory effect, respectively, to the plants (Berg, 1961). Additionally, Maessen et al. (1992) evaluated the effects of pH, Al^{3+} , and the $\text{Al}^{3+}/\text{Ca}^{2+}$ ratio on some species of acid-tolerant and intolerant aquatic plants and

found that neither the addition of Al nor the values of $\text{Al}^{3+}/\text{Ca}^{2+}$ ratio had any visible effect on the vitality of the plants. These authors concluded that the disappearance of the plant species investigated in soft-water after acidification was not due to intoxication by Al, but to a direct effect of the proton load of the environmental water.

In fact, according to Gensemer and Playle (1999), the most important environmental factor controlling Al^{3+} toxicity in algae is pH. The solubility and specificity of Al^{3+} are directly controlled by pH, so at a minimum, the total effect of nominal exposures to dissolved Al^{3+} will change as a function of pH. Given this, Al^{3+} should be more toxic at lower pH values given exposure to a fixed amount of Al^{3+} , because the presumably more toxic soluble forms of Al^{3+} become more and more abundant as pH fall below 5.5 (Casierra-Posada and Niño-Medina, 2007). Despite these reports, the growth of *E. crassipes* in the La Playa reservoir, where the pH of the water is 4.93 ± 1.18 has been observed without any inhibitory effect of pH on the growth of plants as reported by Berg (1961) and corroborated by the results of the current study.

Effect of Al^{3+} on leaf area

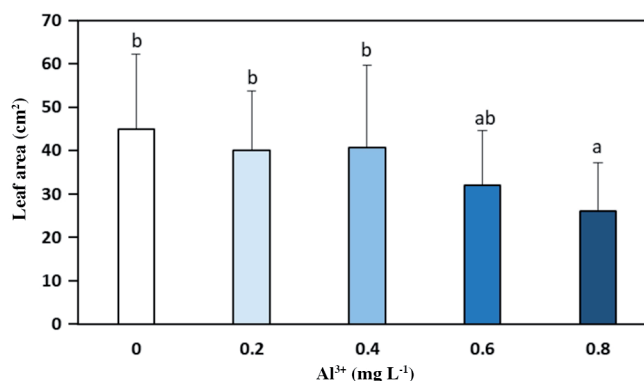
The average values of leaf area were inversely proportional to the increase in the content of Al^{3+} in the aqueous medium. Plants exposed to 0.4, 0.6, and 0.8 mg L^{-1} Al^{3+} had a reduction in leaf area of 9.75%, 28.77%, and 41.88%, respectively, in relation to control plants (Figure 1), with differences that were significant. Colodetti et al. (2015) found that foliar area in *Crambe abyssinica* plants suffered a drastic reduction as a consequence of exposure to Al^{3+} , a result that was observed even when plants were exposed to the lowest concentration of the metal studied in this experiment. Thus, these authors state that this variable resulted in an exponential decrease with increasing Al^{3+} concentration.

Effect of Al^{3+} on evapotranspiration

The amount of evapotranspired water increased only in plants exposed to 0.8 mg L^{-1} Al. In this treatment, the average evapotranspired water per plant was 18.27% greater than in control plants. Only this treatment presented significant differences with the other treatments including the control treatment (Figure 2). Bialowiec et al. (2014) mention that evapotranspiration and evaporation can cause the accumulation of pollutants. It can be inferred in the current study that intake and accumulation of Al in the aerial part of the plants increased by the joint action of the highest dose evaluated (0.8 mg L^{-1} Al^{3+}) and the evapotranspiration that increased with that level of the metal in the medium. However, despite these apparently unfavorable conditions for the plants, growth variables did not show significant differences, demonstrating the tolerance of *E. crassipes* plants to the Al^{3+} levels evaluated.

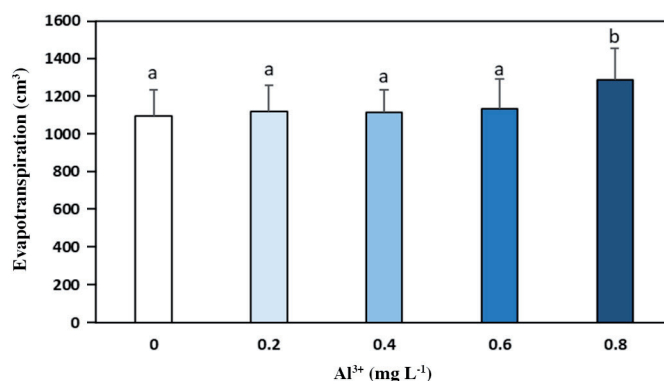
As a consequence of the toxic effect caused by heavy metals in plants, the photosynthetic apparatus is severely affected which alters stomatal conduction, rate of transpiration, and exchange of gases associated with internal C. This can also influence the amount of pigments in the plastids, thereby affecting photosynthesis (Fu and Wang, 2015). Additionally, Dorneles et al. (2019) report Al^{3+} tolerant genotypes which show higher values of WUE and transpiration rate in control conditions (without being exposed to Al^{3+}), compared to Al^{3+} sensitive genotypes.

Figure 1. Average value of leaf area in *Eichhornia crassipes* (Pontederiaceae) plants affected by Al in the aqueous substrate.



Different letters on the columns imply a significant difference according to Tukey's HSD test ($P < 0.05$). Bars represent standard deviation.

Figure 2. Average value of evapotranspiration in *Eichhornia crassipes* (Pontederiaceae) plants affected by Al in the aqueous substrate.



Different letters on the columns imply a significant difference according to Tukey's HSD test ($P < 0.05$). Bars represent standard deviation.

Despite a reduction of the leaf area, an increase in the transpiration rate was observed which at first glance be incoherent; however, the great variability in the size of individual leaves and its compensation with the total number of leaves in a plant, have particularly important implications for understanding the adaptation strategy of plants to environmental changes (Wang et al., 2019). The reduction of leaf area under stressful conditions, could be understood as an adaptive morphological strategy, with the purpose of reducing the loss of water by transpiration or to slow down the growth in young leaves.

Small leaves have been found to have value in plants evolved for warm environments. This knowledge has the potential to enrich vegetation models, in which leaf temperature and water balance during photosynthesis play a key role and can potentially contribute to the understanding of biogeographic trends in relation to the size of leaves (Wang et al., 2019). Yates et al. (2010) point out that leaves of reduced size have thin boundary layers that facilitate transpiration in conditions of high humidity. Thus, high transpiration rates when water is available can facilitate the acquisition of nutrients. Leaves with a reduced area achieve a high transpiration capacity when the demand for evaporation is low and water is abundant. This can be a particularly important strategy for driving the flow of mass of nutrients to plant roots. This finding is of great relevance in the case of the current study since the Al stress induced in the *E. crassipes* plants stimulated the transpiration rate. This was especially the case with the highest concentration of the metal in order to transport the necessary nutrients to maintain plant growth despite the abiotic stress induced by Al³⁺, as observed in Table 1.

Table 1. Average value of the variables involved in the growth of *Eichhornia crassipes* (Pontederiaceae) plants affected by Al in the aqueous substrate.

Variable	Aluminum in aqueous solution (mg L ⁻¹)				
	0.0 (control)	0.2	0.4	0.6	0.8
Total dry matter, g	1.03a	0.99a	1.10a	1.02a	1.00a
Water use efficiency, g L ⁻¹	0.94a	0.89a	0.98a	0.91a	0.79a
Relative growth rate, g g ⁻¹ d ⁻¹	0.01a	0.01a	0.01a	0.01a	0.01a
Absolute growth rate, g d ⁻¹	0.50a	0.49a	0.46a	0.47a	0.47a
Dry matter partitioning					
Leaves, %	22.86a	22.36a	21.01a	21.42a	21.32a
Petioles, %	37.09a	37.02a	36.42a	37.11a	35.59a
Roots, %	40.04a	40.61a	42.56a	41.45a	43.07a
Leaf weight ratio	0.22a	0.22a	0.21a	0.21a	0.21a
Root to shoot ratio	0.67a	0.69a	0.75a	0.73a	0.77a

Means with same letters showed nonsignificant difference according to Tukey's HSD test ($P < 0.05$). Bars represent standard deviation.

The loss of large volumes of freshwater as a consequence of their invasion by *E. crassipes*, can be three times higher in lakes when compared to these water sources without the presence of this aquatic weed. The increase in water loss through evapotranspiration caused by this plant is considered one of the most important aquatic weed problems in freshwater sources. The loss of water by evapotranspiration caused by this floating plant when covering an area greater than 20% of the water surface can be greater than 8000 m³ d⁻¹ (Sasaqi et al., 2019). In accordance with the results of the current study, the presence of dissolved Al in the water of rivers and lakes would increase the evapotranspiration rate (Figure 2), which would compound the impact of this weed on water sources.

Leaf area ratio reduction

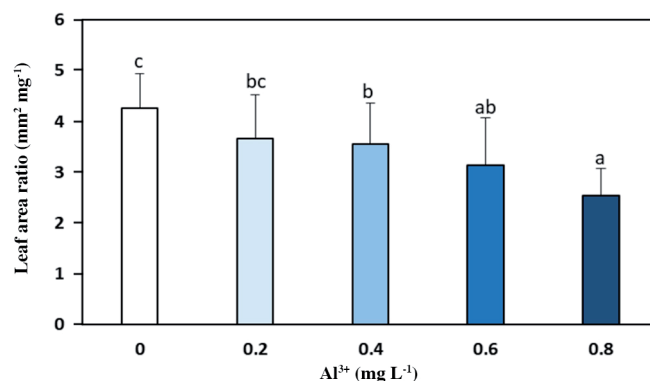
The value found for the leaf area ratio (LAR) decreased inversely proportional to the increase in the Al content in the water, with significant differences. Statistically, the values found in plants exposed to 0.4, 0.6, and 0.8 mg L⁻¹ Al³⁺ stand out, which had LAR values of 16.71%, 26.33%, and 40.41%, respectively, below the values of control plants at the end of the study (Figure 3). Considering that total dry weight per plant had nonsignificant difference, it can be inferred that the reduction in LAR was a consequence of a decrease in foliar area because of the increasing concentration of Al³⁺ in the water.

Since the LAR indicates the efficiency with which a plant uses its leaves to produce plant material; LAR shows the ability of a plant to form a photosynthetic surface. In *Paulownia* spp. plants, this value increased slightly after treatment with the highest concentrations of Cd and Pb, but when the plants were exposed to increasing levels of Zn, there was a reduction in LAR (Miladinova et al., 2014). In contrast, Kabir et al. (2010) found that LAR had an inversely proportional behavior in *Thespesia populnea* plants exposed to different concentrations of Pb. In the particular case of Al toxicity, Colodetti et al. (2015) found that the LAR recorded in *Crambe abyssinica* plants exposed to increasing Al concentrations decreased with the addition of the metal up to a concentration of 78 mg Al³⁺ dm⁻³. After that concentration, a small increase in the value of LAR was observed. These authors point out that toxicity of Al induces a competition between the development of the foliar area and DM production in the plants under study. As a result, only slightly higher values were recorded at high concentrations of Al³⁺ due to the severe problems caused by Al³⁺ to biomass production which becomes more serious than the damage caused in foliar area.

Decrease in the value of specific leaf area

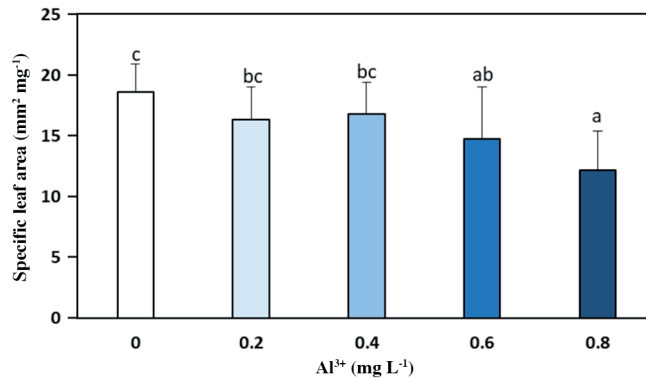
The specific leaf area (SLA) ratios obtained at the end of the study were significantly reduced as Al content increased in the aqueous medium in which the plants grew. In plants treated with 0.4, 0.6, and 0.8 mg L⁻¹ Al, SLA was reduced to 9.90%, 21.01%, and 34.61%, respectively, compared to control plants (Figure 4). Likewise, Colodetti et al. (2015) found that SLA in *C. abyssinica* plants decreased with the addition of 83 mg Al³⁺ dm⁻³; beyond that value, SLA increased slightly. These authors explain this finding with the fact that exposure to Al³⁺ induces thicker and irregularly shaped leaves. When Al³⁺ content is increased, the formation of leaves is affected and the few leaves that develop accumulate very little biomass causing an increase in the values of specific leaf area.

Figure 3. Average leaf area ratio calculated in *Eichhornia crassipes* (Pontederiaceae) plants affected by Al in the aqueous substrate.



Different letters on the columns imply a significant difference according to Tukey's HSD test ($P < 0.05$). Bars represent standard deviation.

Figure 4. Average value of the specific leaf area calculated in *Eichhornia crassipes* (Pontederidaceae) plants affected by aluminum in the aqueous substrate.



Different letters on the columns imply a significant difference according to Tukey's HSD test ($P < 0.05$). Bars represent standard deviation.

Variables unaffected by Al³⁺

The variables which were analyzed in response to the treatments included total DM per plant, WUE, relative growth rate (RGR), absolute growth rate (AGR), DM partitioning in the different organs of the plants, and LWR and R/S. There was nonsignificant difference in any of these variables. The standard deviation for all the treatments, of each variable, was 0.04 g for total DM per plant, 0.2 g L⁻¹ for WUE, 0.002 g g⁻¹ d⁻¹ for RGR, and 0.07 g d⁻¹ for AGR. The DM partitioning in the different organs of the plants showed a standard deviation value of 3.1% for leaves, 4.4% for petioles, and 5.6% for roots. Likewise, a standard deviation of 0.03 was found for LWR value and 0.1 for R/S (Table 1). These results indicate that *E. crassipes* plants have a high phenotypic plasticity which allows them to tolerate high Al levels in the water where they grow. While some metals are toxic to plants only in high concentrations, others such as Al, are only known for their toxic effect on plants (Hodson, 2012). In fact, according to Broadley et al. (2007), heavy metals can affect plants in many ways and the consequences of exposure to these metals are unpredictable and depend on factors such as the type of ion and its concentration, combinations of the different elements in the environment of the plant, the plant, and its development stage.

Gensemer and Playle (1999) point out that in the case of submerged aquatic plants, the probable site of Al³⁺ absorption is the root system. There is also the possibility of some absorption through the leaves in particular cases, however this is not the case since it is a floating plant. The absorption of Al³⁺ in *E. crassipes* occurs through the roots since they are submerged in the aqueous medium as mentioned by Ali et al. (2020). Ali et al. (2020) also point out that the active transport of heavy metals in free-floating aquatic plants occurs from roots where the metals are transferred to other parts of the plant's body. Passive transport is associated with the direct contact of the plant body with the polluting environment. In passive transport, heavy metals accumulate mainly in the upper parts of the plant. According to Gensemer and Playle (1999), in general there is little evidence that Al³⁺ itself has any influence on the community structure of macrophyte species, even in acidified lakes with higher concentrations of Al³⁺. Aluminum tolerant plants are also likely to be H⁺ tolerant plants, with pH as the main variable. Some species will bioaccumulate Al³⁺ and plants in the most acidic sites generally contain the highest tissue content.

Tolerance of plants to Al³⁺

The first noticeable symptom of toxicity, after the plants are exposed to Al³⁺ is a reduction of root growth (Casierra-Posada and Aguilar-Avenidaño, 2007). Similarly, Pereira (2018) mentions that tolerance to Al³⁺ in *Triticum aestivum* is evaluated mainly in hydroponic solutions which expose the plants to solutions with and without this metal as the dependent variables. The relative length of root, the relative weight of root, and regrowth of root which are indicators of tolerance to Al³⁺ were evaluated. As a result, the tolerance of *E. crassipes* can be inferred since DM assigned to the roots did not show significant differences (Table 1). Additionally, a widely known symptom in plants exposed to Al³⁺ is a reduction in production of DM in the roots. Therefore, Freitas et al. (2016) used this parameter to evaluate tolerance to Al³⁺ in rice plants grown in nutrient solution. These authors also point out that before the decrease in DM content in the root occurs as a consequence of Al³⁺, this phytotoxic metal first reduces the elongation of the root resulting in shorter roots.

In the current study, nonsignificant difference was found in DM partitioning or in total DM content per plant (Table 1) which is another way of determining the tolerance of *E. crassipes* plants to the harmful effects of Al. Freitas et al. (2016) used root and shoot DM production as variables to determine tolerance of rice plants grown in nutrient solutions with and without Al³⁺.

Using a hydroponic system with a nutrient solution, Dorneles et al. (2019) identified Al³⁺ tolerant *Solanum tuberosum* genotypes that presented higher WUE and transpiration rates in control treatments when compared to Al³⁺ sensitive plant materials. The current study did not show significant differences in WUE, but it did increase transpiration, especially with exposure of plants to 0.8 mg L⁻¹ Al³⁺. Consequently, these results also support that studied plants have sufficient phenotypic plasticity to tolerate the negative effects of Al³⁺.

In accordance with the proposals by Hunt et al. (2002), growth rates are fundamental variables to quantify biological productivity and evaluate the form and function of plants exposed to a demanding environmental supply. Similarly, Ludwig et al. (2010) point out that RGR is a relevant tool to infer the adaptation of plants that develop in stressful environments given that RGR is an indicator of efficiency.

Nascimento et al. (2016) evaluated the effect of a soil contaminated with Pb²⁺ on four cultivated species. The similarity of Pb²⁺ with Al³⁺ is that both are considered heavy metals. In their study, related to the RGR, these authors found that when growth rates are correlated with other growth data, it can be inferred that the negative values of RGR and net assimilation rate represent the consumption of reserves to satisfy a greater demand for energy for the maintenance of the plant created by the stress caused by this heavy metal. This shows that, under field conditions, the species in which these growth variables were negatively affected do not have the same tolerance as those in which these variables remained unaltered by Pb²⁺. Therefore, RGR and AGR are a determining tool when evaluating tolerance of plant species. Consequently, tolerance of *E. crassipes* to Al³⁺ concentrations evaluated in the current study can be assumed, based on the fact that nonsignificant difference was found in RGR, AGR, and DM partitioning (Table 1).

A significant correlation has been shown between low pH and high Al³⁺ concentrations in acidified fresh water where this metal can reach levels of 0.3 to 1.6 mM (0.008-0.043 mg L⁻¹) and cause a serious metabolic disorder in some hydrophytes (Dickson, 1978; Pettersson et al., 1985). However, in the current study, floating plants of *E. crassipes* showed inversely proportional effects to the content of Al³⁺ in the aqueous substrate, in variables such as leaf area (Figure 2), LAR (Figure 3), and SLA (Figure 4). Despite these effects caused by Al, total dry weight, growth rates, and WUE were unaffected (Table 1). Ali et al. (2020) pointed out that many aquatic plants have the ability to resist a high load of toxic metals present in polluted waters without showing apparent signs of a significant reduction in the production and accumulation of biomass, nor a decrease in values of the variables involved in the evaluation of plant growth. Therefore, the adaptive success of this aquatic weed is a result of its phenotypic plasticity, fostered by the anthropic alteration of the physicochemical composition of water sources.

CONCLUSIONS

Among the variables evaluated, the variable affected the greatest due to the addition of Al³⁺ was leaf area, which also affected the values of the variables associated with growth. However, the plants were able to adapt through an increase in the evapotranspiration rate in order to increase the uptake of nutrients in addition to the water uptake by the roots. This helped maintain the values of growth rates, water use efficiency, and DM accumulation despite the stress conditions induced by the presence of Al³⁺. On the other hand, Al content found in water sources in Colombia, despite being in the ranges reported as toxic for some aquatic plants, did not significantly affect the growth of *Eichhornia crassipes* plants. This is due to the fact that this weed and its ability to adapt as well as anthropogenic changes in the physicochemical composition of water sources have allowed it to invade and thrive in fresh water sources without Al in the concentrations evaluated, representing a risk for its growth. As a result, it was possible to understand that the evaluation of the growth of these plants under controlled conditions similar to those found in its natural habitat. This allowed us to infer that this weed is a very successful plant in the invasion of water sources given its ability to adapt to an unfavorable environment related to Al³⁺ toxicity.

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