



Root Restriction Effects on Physiology of *Zantedeschia aethiopica*

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Authors' contributions

This work was carried out in collaboration between all authors. Authors ADB and EG designed the study and wrote the manuscript. Authors MP, JM and AP recorded data, performed the statistical analysis, managed the analyses of the study. All authors read and approved the final manuscript.

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ABSTRACT

Previous results from ornamental plants suggest that shoot biomass accumulation is a function of roots biomass. The possibility of cropping *Zantedeschia aethiopica* from seeds in either greenhouse-amended soils or pot substrates allow for quantify the effect of a root restriction on growth and plant quality. The root restriction syndrome has been related to an insufficient cytokinin supply from roots but the physiological mechanisms involved in geophyte ornamental plants are lacking. The aim of this work was to characterize seedling *Z. aethiopica* growth under two different root restrictions environments (greenhouse-amended soils or pot substrate) and the effect of a single 6, benzyl amino purine (BAP) spray on the hypothesis that the lesser root restriction the higher both post-transplant fresh-dry weight accumulation and leaf area expansion. Results showed a higher fresh-dry weight, leaf area and leaf number in plants from pots with a *Sphagnum*

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magellanicum peat-base substrate. A single BAP spray increased responses mainly in pot-grown plants. Positive relationships between the rate of leaf area expansion (RLAE), the leaf appearance rate (RLA), the relative growth rate (RGR), the net assimilation rate (NAR) and root dry weight were found. These results showed that a root restriction related to substrate compaction in pots has a lesser impact on *Z. aethiopic* plant growth than a root restriction related to compaction in soils, which cannot be overridden by a single 100 mg L⁻¹ BAP spray.

Keywords: Amended soil environment; cytokinins; ornamental geophyte plant; potted plants.

1. INTRODUCTION

Zantedeschia aethiopica (calla lily) is a perennial plant grown for the production of cut flowers, which has been used as seasonal outdoor garden plants in amended soils for many years and, recently as potted flowering plant [1,2]. Rhizomes is the structure, which survives to native areas during dry periods. Rhizomes are produced by specialty propagators in the field under different amended soils, sold to commercial growers and grow the plant as a flowering potted plant or for cut flowers [3]. After rhizome sprouting, plant height, leaf number and leaf area increased as far as 210 days, while the leaf growth was accelerated, stabilizing after 90 days. Rhizomes grew steadily after 120 days from sprouting. The period of the greatest dry matter accumulation in shoots occurred in the first months after transplantation, possibly due to the need to increase the leaf surface. The proportional dry matter accumulation between shoots and rhizomes was reversed: while a reduction was observed the shoots over time, rhizomes showed increased dry mass accumulation [4]. As opposed to other *Zantedeschia* species, *Z. aethiopica* developed viable seed, which are ruled out for commercial propagation.

Root system architecture influences nutrient and water uptake efficiency and thus plant growth and productivity [5]. Roots usually suffer greater exposure to multiple abiotic stresses than shoots. Therefore, the root system can be as affected, or even more affected, than the aerial parts of a plant by such stresses. Root system development is affected by soil conditions. In addition, root elongation is more influenced by mechanical and physical properties rather than chemical properties of soil [6]. Variations in root development were best explained by the variation in penetration resistance, rather than other soil properties. Increased soil penetration resistance reduced the root elongation rate, especially for thick roots. In addition, the branching pattern was affected [7]. Mechanical

impedance is the major limitation to root elongation in many field soils [8]. It has been indicated that root plasticity responses allow plants to forage with precision from a spatially and temporally heterogeneous environment, minimizing the metabolic cost of soil exploration by matching plant investment in root biomass and root function of resource supply to soil [9]. Bassett et al. [10] found that compaction reduced the number and speed at which the Araceae *Cordyline australis* (Forst. f.) seedlings roots penetrated the soil. Reductions in elongation rate resulting from difficulty in generating sufficient force for roots to displace soil particles and extend over the spaces created.

In the same way than field soil compaction, root restriction may occur whenever pot sizes or rooting volume is physically limited. Poorter et al. [11] showed that doubling the pot size, biomass production increased by 43%. Root restriction decreased leaf number, leaf area and dry matter of shoots and roots, while increasing shoot-to-root dry matter ratio. Plants in compacted plots had a greater concentration of roots near the base of the plants than that in the plants in the zero-load plots. Plants in the subsoiled plots had fewer roots concentrated near the base of the plant over the plants in the non-subsoiled plots of each load [12]. There is few reports on the effect of soil restriction on geophyte perennial plants [13], but *Z. aethiopica* research on growth development in relation to soil conditions is lacking.

The root restriction response is due to the changes in various root to shoot communication events, with concomitant changes in physiological processes. These potential signaling events can be broadly classified as hydraulic (water) and non-hydraulic in nature. Non-hydraulic factors may include nutrient uptake and low oxygen availability and endogenous phytohormone levels [14]. There have been numerous studies published in the last few years describing and discussing the chemical and hormonal bases for the responses

of roots to abiotic stresses. Although the morphological adaptations of plants are largely different from diverse abiotic stresses, similar hormones and biochemical processes are involved in signaling from roots to the shoot during different stress responses [15,16].

The objective of this work was to describe *Z. aethiopica* seedling growth under different root restriction degrees such as the observed in both greenhouse soil amended and pots filled with a *Sphagnum* peat-base under the hypothesis that a single post-transplant 6, benzyl amino purine (BAP) spray is a commercial tool for overriding root restrictions effects.

2. MATERIALS AND METHODS

2.1 Plant Material and Experimental Design

The experiment was carried out in a greenhouse at the Faculty of Agronomy, University of Buenos Aires, Argentina (34°28'S), from October 5th 2013 to March 25th 2014. The greenhouse was covered with a neutral black shade-cloth (for 50% full sunlight) (Agriplast S.A. Buenos Aires, Argentina).

Zantedeschia aethiopica seeds were germinated and grown in 50-cells plug trays (55.70 cm³ cell⁻¹) in a Klasmann 411® medium (Klasmann-Deilmann, GmbH, Germany). When seedlings reached the transplant stage, they were transplanted into two different greenhouse locations:

- Plants were transplanted to 3-liter pots containing *Sphagnum maguellanicum* peat-river waste-perlite (40-40-20, v/v/v) substrate (**P**).
- Plants were transplanted to a greenhouse soil amended with *Sphagnum maguellanicum* peat (**S**).

One week from transplant, seedlings were sprayed with different single BAP (6-benzyl amino purine) (SIGMA EC 214-927-5) (Sigma-Aldrich Co., St. Louis, MO, USA) solutions (0, 50 or 100 mg L⁻¹). BAP was previously diluted in alcohol 80% and plants were run-off sprayed.

A weekly ferti-irrigated solution with 1.0: 0.05: 1.0:0.5 (v/v/v/v) N: P: K: Ca (nitric acid, phosphorus acid, potassium nitrate, and calcium nitrate; Agroquímica Larrocca S.R.L., Buenos

Aires, Argentina) through the overhead irrigation water (100 mg L⁻¹ N) was included.

Daily mean temperatures (18.27 to 25.86°C) and daily photosynthetic active radiation (6.83 to 11.16 mole photons m⁻² day⁻¹) were recorded with a HOBO sensor (H08-004-02) (Onset Computer Corporation, MA, USA) connected to a HOBO H8 data logger. The plants were arranged at a density of 10 plants m⁻², which avoided mutual shading.

Samples of both substrate and a greenhouse-amended soil were collected at the beginning of the experiment and physical and chemical properties were determined according to Fonteno [17].

Plants for destructive measurements were harvested (five per treatment and block) at the transplant stage and at 30-day intervals during the experiment. Roots were washed and rhizome, root, stem, leaf and petioles fresh weights (FW) were recorded. Dry weights (DW) were recorded after drying rhizome, roots, stems, leaves and petioles to constant weight at 80°C for 96 hours. The number of leaves was recorded and each leaf area was determined using a leaf area meter LICOR FL16 (LI-COR Inc., Lincoln, NE, USA).

2.2 Data Analysis

The rate of leaf area expansion (RLAE) was calculated as the slope of the regression of the natural logarithm of total leaf area versus time (in days). The rate of leaf appearance (RLA) was calculated as the slope of the number of fully expanded leaves versus time (in weeks). The relative growth rate (RGR) and the rhizome relative growth rate (RRGR) were calculated as the slope of the regression of the natural logarithm of the whole plant or rhizome on a DW basis versus time (in days). The mean net assimilation rate (NAR), and the leaf area ratio (LAR) were calculated as follows:

$$NAR = \frac{k_w W_0 e^{k_w t}}{A_0 e^{k_a t}}$$

$$LAR = k_a / \frac{A_a e^{k_a t}}{k_w W_0 e^{k_w t}}$$

where: kw: RGR (days); W₀: extrapolated value of total dry weight at time zero (g); A₀:

extrapolated value of leaf area at time zero (cm^2); ka: RLAE (days); t: time (days) at the midpoint of the experimental period and e: base of natural logarithms.

The specific leaf area on a FW basis (SLA) and leaf weight rate (LWR) were calculated as the ratio between the area of the new individual leaf and leaf FW and the ratio between the leaf DW and the total plant DW respectively.

The allometric coefficients between root and shoot and between leaf blades + petiole and the stem fraction were calculated as the slope (β) of the straight-line regression of the natural logarithm of the root DW versus the natural logarithm of the shoot DW and between the natural logarithm of the leaf blade + petiole DW versus the natural logarithm of the stem DW respectively.

2.3 Statistical Analysis

We used a complete aleatory design with three blocks of thirty replications each ($n = 3$). Data were subjected to two-way analysis of variance and means were separated by Tukey's test ($P < 0.05$); STATISTICA 8 (StatSoft) software was used. Slopes from straight-line regressions of RLA, RLAE, RGR, NAR, LAR, SLA, LWR and allometric values were tested using the SMATR package [18].

3. RESULTS

3.1 Physical and Chemical Properties of the Substrate

The *Sphagnum maguellanicum* peat-base substrate showed, at the beginning of the experiment, higher total porosity, air filled-porosity and water holding capacity than the greenhouse-amended soil. On the contrary, higher density and electrical conductivity (EC) from S were found.

3.2 Fresh Biomass Accumulation and Leaf Area

After six months of the beginning of the experiment, potted *Z. aethiopica* plants showed higher total fresh weight accumulation than those grown in a greenhouse-amended soil. On the other hand, the higher BAP doses the higher FW in plants grown in pots filled with an organic substrate was found (Fig. 1a). No significant differences in both shoot and root FW in BAP-sprayed plants from a greenhouse-amended soil

were found. When the mean aerial FW was plotted against the mean root FW (Fig. 1b), a positive correlation was found ($r^2 = 0.997$; $P < .001$). Pot plants gave the higher values.

Plants from S did not develop a visual rhizome. On the hand, control plants cropping in pots filled with a *Sphagnum maguellanicum* peat-base substrate showed a clear rhizome starting 60 days of the beginning of the experiment, which increasing with time. The higher BAP sprays concentration doses the higher rhizome FW (Fig. 2).

Control pot *Z. aethiopica* plants showed higher both total (Fig. 3a) and individual (Fig. 3b) leaf area than those cropping in a greenhouse-amended soil. In both soil environment, the higher response was found in plants sprayed with 100 mg L^{-1} BAP.

Control *Z. aethiopica* plants grown in pots showed higher RLAE, RLA and LWR significant values and lower SLA values than those grown in an amended soil. The higher BAP concentration, the higher RLAE, RLA, LWR and the lower SLA (Table 2).

3.3 Growth Rates and Root Dry Weight Relationships

Significant RGR differences between pot and greenhouse-amended soil plants were found. The higher BAP concentration, the higher RGR. When RGR was disaggregated in NAR and LAR, the same response pattern was found from NAR but no significant differences in LAR. Only plants from pots developed a rhizome, the higher BAP concentration, the higher RRGR (Table 3).

When plotting the data from all treatments, we found a close direct relationship ($r^2 = 0.987$) between RGR and NAR (Fig. 4a) and an inverse relationship between RGR and LAR ($r^2 = 0.769$) (Fig. 4b), between RGR and SLA ($r^2 = 0.713$) (Fig. 4c) and between SLA and NAR ($r^2 = 0.707$) (Fig. 4d). Nevertheless, a clear difference between pot plants and those grown in a greenhouse-amended soil were ever found.

Positive relationships between RLAE ($r^2 = 0.719$) (Fig. 5a), RLA ($r^2 = 0.974$) (Fig. 5b), RGR ($r^2 = 0.951$) (Fig. 5c), NAR ($r^2 = 0.986$) (Fig. 5d) and root DW but, a negative relationship between SLA and root DW ($r^2 = 0.738$) (Fig. 5e) were found. Once again, a clear difference between pot plants and those grown in a greenhouse-amended soil were ever found.

Table 1. Physical and chemical characteristics of both pot substrate (P) and greenhouse-amended soil (S). Different lower-case letters indicate significant differences ($P < .05$) between P and S

	Total porosity (%)	Air-filled porosity (%)	Density (g dm^{-3})	Water holding capacity (g cm^{-3})	pH	EC dSm^{-1}
P	67.53 ^a	23.27 ^a	0.21 ^b	0.43 ^a	6.49 ^a	0.017 ^b
S	25.02 ^b	5.60 ^b	0.90 ^a	0.32 ^b	6.09 ^a	0.160 ^a

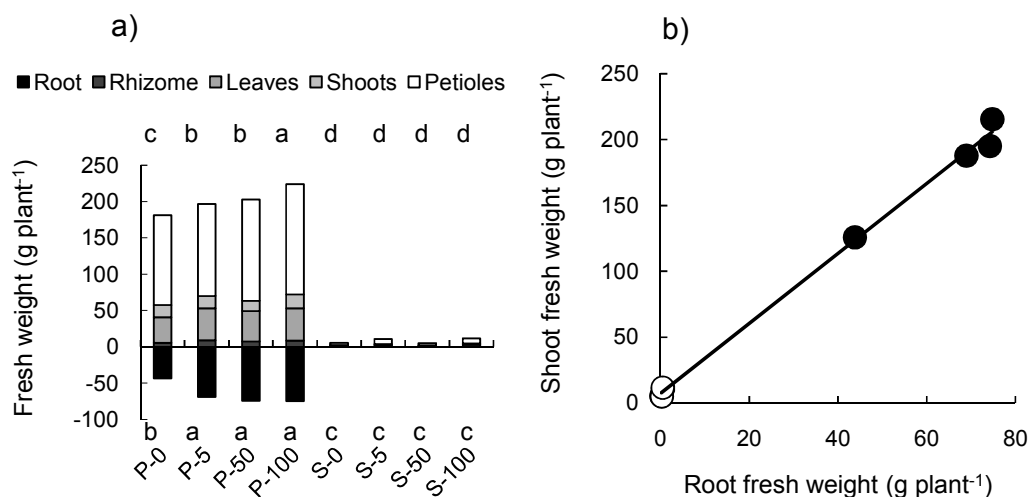


Fig. 1. Panel a. Accumulated fresh weight at the end of the experiment (210 days of cropping) in *Z. aethiopica* plants cropped in pots (P) (full symbols) or in an greenhouse-amended soil (S) (empty symbols) and sprayed with different post-transplant BAP spray concentrations (0, 5, 50 or 100 mg L^{-1}). Different lowercase letters indicate significant differences ($P < .05$) between control and BAP-sprayed plants. Panel b. Relationships between shoot and root fresh weight. The straight-line regression was $\text{Shoot FW} = 2.66 \text{ Root FW} + 7.22$ ($r^2 = 0.997$). The probability of the slope being zero was $P < .001$

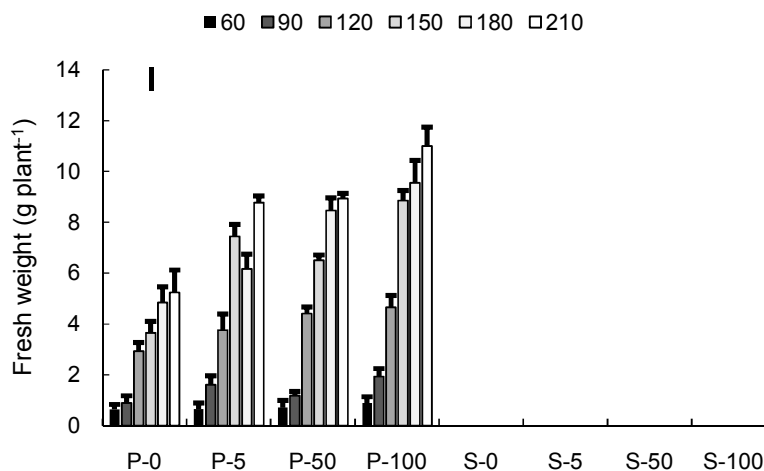


Fig. 2. Changes in *Z. aethiopica* rhizome fresh weight during the experiment for plants cropping in pots (P) or in a greenhouse-amended soil (S) and sprayed with different post-transplant BAP spray concentrations (0, 5, 50 or 100 mg L^{-1}). Standard errors are indicated. Vertical lines indicate least significant differences (LSD)

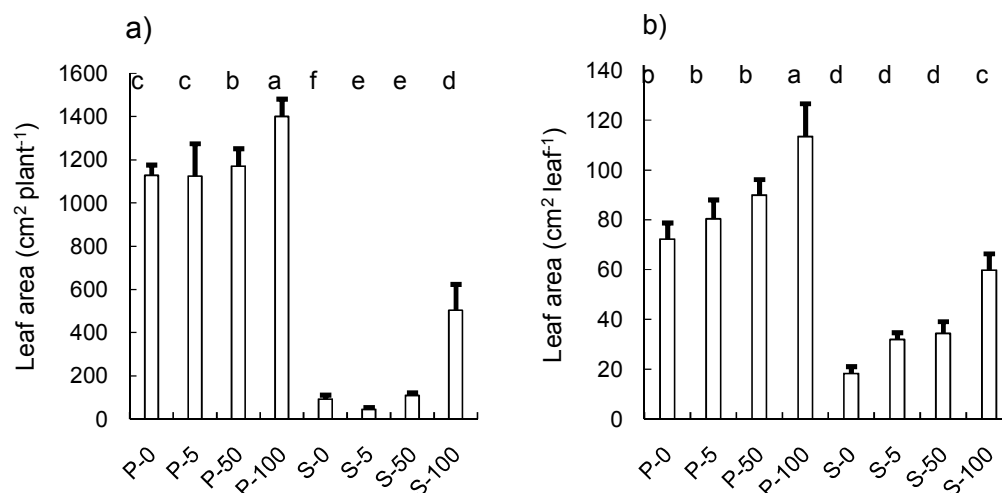


Fig. 3. Total leaf area (a) and mean individual leaf area (b) at the end of the experiment in *Z. aethiopica* plants cropped in pots (P) or in a greenhouse-amended soil (S) and sprayed with different post-transplant BAP spray concentrations (0, 5, 50 or 100 mg L⁻¹). Different lowercase letters indicate significant differences ($P < .05$) between control and BAP-sprayed plants

Table 2. Changes in RLAE, RLA, SLA and LWR in *Z. aethiopica* plants cropped in pots (P) or in a greenhouse-amended soil (S) and sprayed with different post-transplant BAP spray concentrations (0, 5, 50 or 100 mg L⁻¹). Different lowercase letters indicate significant differences ($P < .05$) between control and BAP-sprayed plants. Different capital letters indicate significant differences ($P < .05$) between P and S grown plants for each BAP application. The probability of the slope being zero for RLAE, RLA, SLA and LWR was $P < .001$

BAP (mg L ⁻¹)	RLAE (cm ² cm ⁻² day ⁻¹)		RLA (leaves week ⁻¹)		SLA (cm ² g ⁻¹)		LWR (g g ⁻¹)	
	P	S	P	S	P	S	P	S
0	0.0240 ^{bA}	0.0099 ^{cB}	0.0577 ^{cA}	0.0043 ^{cB}	244.84 ^{aB}	327.12 ^{aA}	0.233 ^{bA}	0.210 ^{cB}
5	0.0252 ^{aA}	0.0112 ^{bB}	0.0609 ^{bA}	0.0055 ^{cB}	225.27 ^{bB}	309.26 ^{bA}	0.223 ^{bA}	0.228 ^{cA}
50	0.0258 ^{aA}	0.0117 ^{bB}	0.0660 ^{aA}	0.0077 ^{bB}	210.92 ^{cB}	284.17 ^{cA}	0.236 ^{bB}	0.284 ^{bA}
100	0.0262 ^{aA}	0.0223 ^{aB}	0.0650 ^{aA}	0.0121 ^{aB}	140.74 ^{dB}	247.24 ^{dA}	0.329 ^{aB}	0.484 ^{aA}

Table 3. Changes in RGR, NAR, LAR and RRGR in *Z. aethiopica* plants cropped in pots (P) or in a greenhouse-amended soil (S) and sprayed with different post-transplant BAP spray concentrations (0, 5, 50 or 100 mg L⁻¹). Different lowercase letters indicate significant differences ($P < .05$) between control and BAP-sprayed plants. Different capital letters indicate significant differences ($P < .05$) between P and S grown plants for each BAP application. The probability of the slope being zero for RGR, NAR and LAR was $P < .001$

BAP (mg L ⁻¹)	RGR (g g ⁻¹ day ⁻¹)		NAR (g cm ⁻² day ⁻¹) (x 10 ⁻⁵)		LAR (cm ² g ⁻¹)		RRGR (g g ⁻¹ day ⁻¹)	
	P	S	P	S	P	S	P	S
0	0.0180 ^{bA}	0.0006 ^{cB}	3.23 ^{bA}	0.09 ^{cB}	56.82 ^{aA}	68.09 ^{aA}	0.0218 ^{cA}	0.0000 ^{aB}
5	0.0206 ^{aA}	0.0014 ^{cB}	4.13 ^{bA}	0.22 ^{bB}	50.03 ^{aA}	70.34 ^{aA}	0.0310 ^{bA}	0.0000 ^{aB}
50	0.0212 ^{aA}	0.0031 ^{bB}	4.25 ^{aA}	0.38 ^{aB}	49.24 ^{aB}	80.59 ^{aA}	0.0339 ^{bA}	0.0000 ^{aB}
100	0.0216 ^{aA}	0.0056 ^{aB}	4.65 ^{aA}	0.47 ^{aB}	46.47 ^{aB}	81.90 ^{aA}	0.0410 ^{aA}	0.0000 ^{aB}

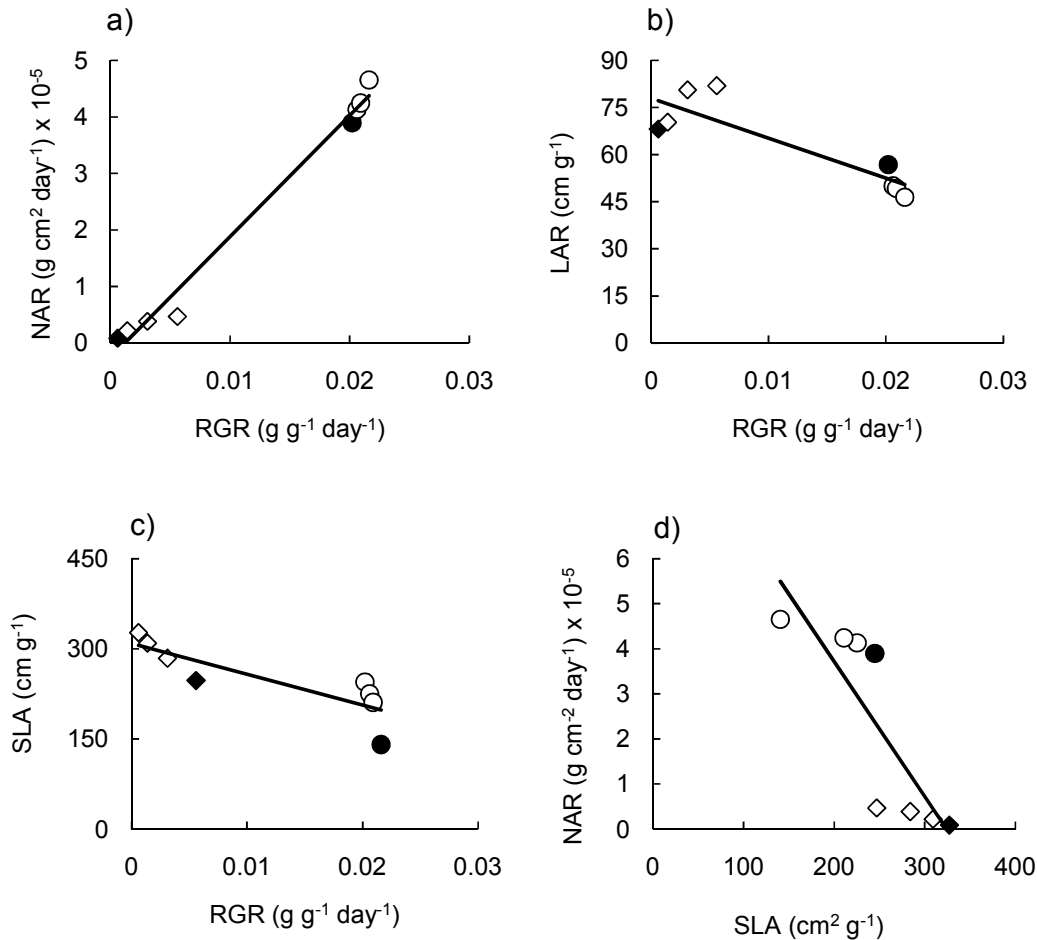


Fig. 4. NAR (a), LAR (b), SLA (c) related to RGR and NAR - SLA relationships (d) in *Z. aethiopia* plants cropped in pots (●, ○) or in a greenhouse-amended soil (◆, ◇) and sprayed with different post-transplant BAP spray concentrations (0, 5, 50 or 100 mg L⁻¹). Control plants: full symbols; BAP-sprayed plants: empty symbols. The straight-line regression were NAR = 214.53 RGR + 0.26 ($r^2 = 0.987$; $P < .001$); LAR = -1270.40 RGR + 77.86 ($r^2 = 0.769$; $P < .001$); SLA = -5111.80 RGR + 308.76 ($r^2 = 0.713$; $P < .001$); NAR = -0.03 SLA + 9.72 ($r^2 = 0.707$, $P < .001$).

Table 4. Changes in allometric relationships between roots and shoots and between leaves + petioles and stems for in *Z. aethiopia* plants cropped in pots or in a greenhouse-amended soil and sprayed with different post-transplant BAP spray concentrations (0, 5, 50 or 100 mg L⁻¹) during the 210 days of the experiment. The slope straight-line (β) and the coefficients of determination (r^2) are indicated. The probability of the slope being zero was $P < .001$. Different lowercase letters indicate significant differences ($P < .05$) between control and BAP-sprayed plants, while different capital letters indicate significant differences ($P < .05$) between pot and greenhouse-amended soil environments

BAP (mg L ⁻¹)	Roots : Shoots				Leaves + petioles: Stems			
	P		S		P		S	
	β	r^2	β	r^2	β	r^2	β	r^2
0	1.089 ^{aB}	0.967	1.124 ^{aA}	0.672	1.233 ^{aA}	0.903	1.136 ^{aB}	0.601
5	1.058 ^{bA}	0.953	0.985 ^{bB}	0.613	1.223 ^{aA}	0.891	1.098 ^{bB}	0.740
50	1.026 ^{cA}	0.940	0.860 ^{cB}	0.570	1.203 ^{bA}	0.912	1.048 ^{cB}	0.628
100	0.995 ^{dA}	0.896	0.761 ^{dB}	0.619	1.196 ^{bA}	0.919	1.004 ^{dB}	0.797

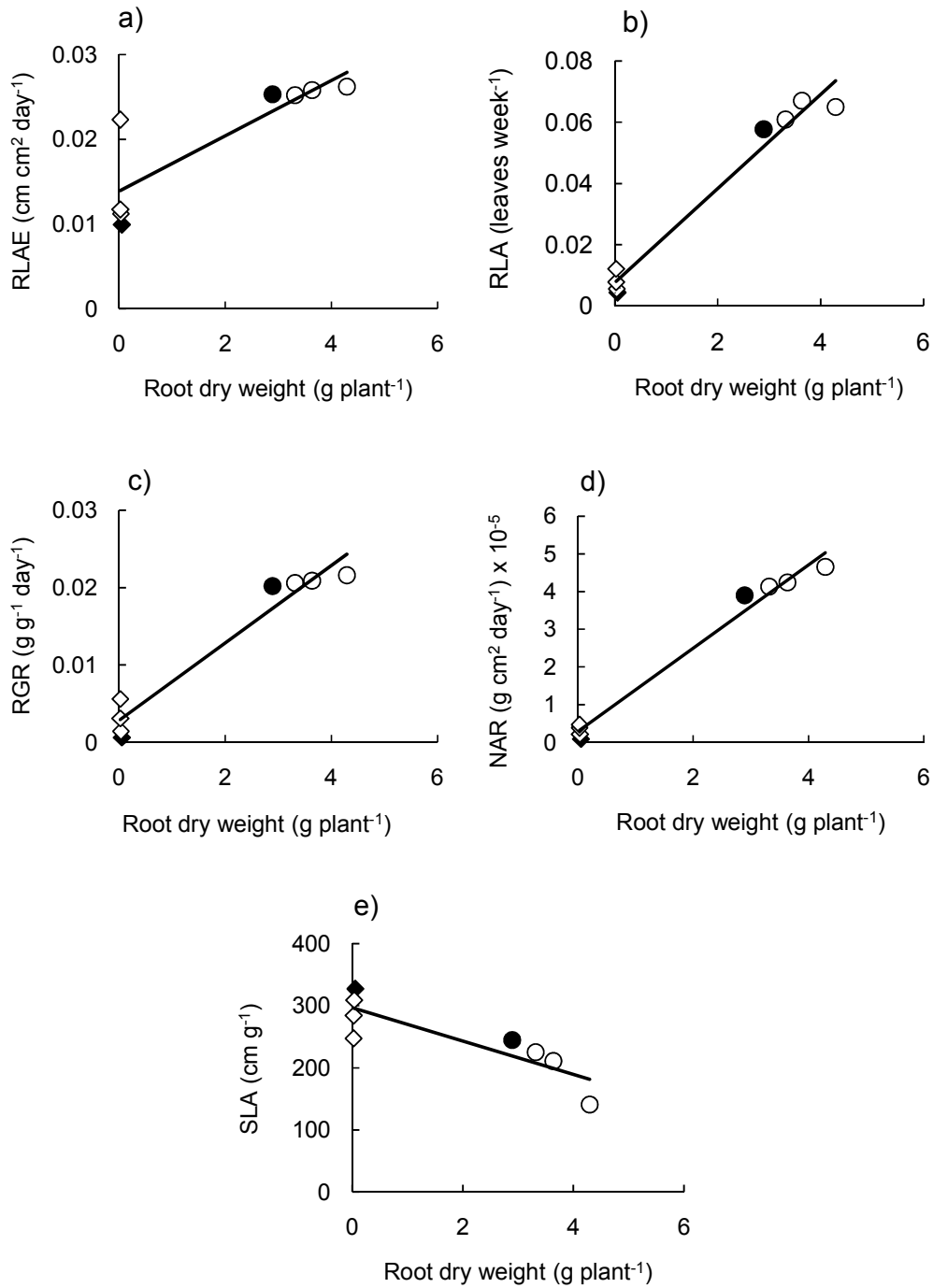


Fig. 5. Relationship between RLAE (a), RLA (b), RGR (c), NAR (d), SLA (e) and the root dry weight (RDW) in *Z. aethiopica* plants cropped in pots (●, ○) or in a greenhouse-amended soil (◆, ◇) and sprayed with different post-transplant BAP spray concentrations (0, 5, 50 or 100 mg L⁻¹). Control plants: full symbols; BAP-sprayed plants: empty symbols. The straight-line regression were RLAE = 0.003 RDW + 0.014 ($r^2 = 0.719$; $P < .001$); RLA = 0.015 RDW + 0.008 ($r^2 = 0.974$; $P < .001$); RGR = 0.600 RDW + 0.003 ($r^2 = 0.951$; $P < .001$); NAR = 1.102 RDW + 0.293 ($r^2 = 0.986$; $P < .001$); SLA = -26.74 RDW + 296.44 ($r^2 = 0.738$; $P < .001$)

3.4 Dry Weight Partitioning

Pot control plants showed lower roots: shoots and higher leaves + petioles: stems slope straight-line coefficients (β) than greenhouse-amended soil. A single BAP spray decreased all β coefficient in both potted plants and greenhouse-amended soil (Table 4).

4. DISCUSSION

Z. aethiopica (calla lily) is an ornamental plant for diverse purposes [19]. Historically, plants cropping to obtain cut flowers were grown in amended field soils but next, *Z. aethiopica* were offered as pot plant and grown in pots filled with different substrates. Table 1 showed that physical properties could be quite different from both locations. Compaction strongly influences soil physical properties such as bulk density, pore size, pore continuity, aeration, permeability, penetration resistance, soil water and temperature regimes [20]. On the other hand, the presence of a root restriction related to pot physical impedance [13,21,22] or both soil and substrate compaction would be override by a single BAP spray [23].

Plant growth is a genetically programmed process but modified by signals from both aerial and edaphic environments, which involved plant hormones and sugar availability and can change biomass accumulation [24]. The importance of root growth of maintaining crop yields is becoming recognized and of increasing interest to plant breeders [25,26]. Becel et al. [7] studied root system plasticity related to soil physic properties and suggested that bulk density had a marked effect on root system development because root growth is reduced in compacted soils. A decrease in resource availability or an increase in bulk density alters the root growth and distribution, so that water and nutrient uptake may be reduced. Hence plant growth can decrease from a reduction in leaf area or dry mass and plant function may be altered (photosynthesis and transpiration).

In their native environments [27], *Z. aethiopica* and the rest of the ornamental Araceae plants slowly increase total biomass because their ecological adaptation to low light availability [28,29]. However, their use for the pot plant industry needs for an increase in biomass accumulation during commercial cropping [30]. On the other hand, photosynthetic active

radiation (PAR) would not be the unique factor, which determine RGR. Our results showed that, at the same non-limiting PAR, plants grown in a substrate with better physical properties (pot substrate) (Table 1) showed higher both total fresh weight (Fig. 1a) and rhizome fresh weight (Fig. 2) than those from the greenhouse-amended soil after six months of cropping. Luria and Weiss [1] suggested that the decrease in rhizome yield by dense planting, which may decrease light penetration, or by leaf removal may be caused by lower levels of assimilates being accumulated by the plants due to reduced total photosynthesis. On the other hand, we found a positive relationship between the aerial FW and the root FW (Fig. 1b), in agreement with our previous results [21,23,31,32].

To avoid the effect of previous growth when rhizome was used for propagation, seedlings from seeds were tested. A single post-transplant BAP spray increased *Z. aethiopica* biomass accumulation (Figs. 1 and 2) in agreement with previous reports [15,33,34]. On the other hand, dipping rhizomes in 350 mg L⁻¹ benzyl adenine increased flower yield (a trait directly related to photo assimilate availability) fivefold over the control [1].

The higher *Z. aethiopica* biomass accumulation in a fresh weight-base could be explained by a higher total leaf area (Fig. 3a), as a combination of a higher individual leaf area (Fig. 3b), RLAE and RLA (Table 2), which indicate strong changes in shoot apical meristem (SAM) growth and development. SAM is responsible for generating all above ground organs [35] and define growth rate and final size of plant organs [36]. It is controlled by hormones, which regulate biosynthesis and transport of other hormones, and by hormone interactions. The latter regulates particular transcription factors, which integrate and coordinate the developmental response. Regulating the meristem growth depends on the mode of manipulating this hormonal cross talk [15]. Several hormones, including auxins, cytokinins, and gibberellins, act both independently and in combination to regulate meristem function [37,38,39,40]. The main function of endogenous cytokinins are to control the cell cycles and SAM growth [41,42], but also in the response to changes in their environment [43].

The possibility to a plastochron decreases (i.e. the time for successive leaf initiation events), would be associated with a higher increase in

apex size [38,44] , the presence of non- limiting sugar availability [45] or a change in the relative assimilation allocation between roots and shoots [46]. Zhu et al. [47] and Lee et al. [48] showed that plastochron, which can be estimated at RLA, could increase in transgenic plants, which root synthesizing a low cytokinin level. Data from Table 2 shown that the lower RLA values were found in *Z. aethiopica* plants with higher root restrictions degree (S) with a significantly increase in both locations (P and S) when a 100 mg L⁻¹ BAP was applied. These results are in agreement with previous reports as in ornamentals [23,38,49] as in vegetables [50, 51, 52).

On the other hand, data from Table 2 showed that different root restriction degree had a higher impact on *Z. aethiopica* RLA than on individual leaf area (Fig. 3b). Although Gonzalez et al. [53] claimed that more research is needed to establish whether a causal relationship exists between SAM size and leaf size, any change in the relative effect of this relationship due to changes in the *KNOX* genes expression could modify individual leaf area [54]. The size of plant organs, such as leaves, is determined by an interaction of genotype and environmental influences as well [55]. Bögre et al. [36] suggested the presence of a compensatory mechanism, which related leaf initiation rate with their final leaf size, in such a way that shoot biomass accumulation remain constant. So that assumption would be true, a few leaves of large size or many but small leaves must be initiated. Our results from *Z. aethiopica* are not in agreement with Bögre et al. [36] but agree with previous results in other ornamental plants [23].

Rahayu et al. [56] suggested that a decrease in cytokinins supplies from roots to shoots would inhibit leaf expansion. A low cytokinin endogenous concentration on SAM would increase root growth and, in this way, root: shoot ratio. Di Benedetto et al. [38, 39, 40] have indicated that as cytokinin (in a direct way) so auxins (in an indirect way through an increase in root branching) could increase growth of other Araceae plants. Auxin affects lateral root positioning, initiation and subsequent development, thereby influencing the whole root system architecture [57]. Root branching is a common and important developmental process for increasing the number of growing tips, which can synthesizing endogenous cytokinins and defining the distribution of the root meristem size [58].

In the present study, due we found no significant differences in the DW content of plants grown at different root restriction degree or BAP-sprayed plants (data not shown), it is possible to describe the photo assimilates acquisition and partitioning rates on a DW base. Higher RGRs was found in plants growing in pots and from BAP-sprayed ones (Table 3). When RGR was disagreed as the product of LAR, the so-called 'morphological component' and NAR, the 'physiological component', which would be associated with an increased efficiency of photosynthetic fixation [59], we found no significant changes in LAR but higher values for NAR in plants cropping in pots (Table 3).

A main factor of biomass accumulation is related to the photosynthetic process because it provides structural material for growth [24]. Young et al. [14] and Franco et al. [16] showed that growing plants in a restricted rooting medium frequently causes a down-regulation in photosynthetic capacity. In agreement, Poorter et al. [11] showed that reduced growth of smaller pots was caused mainly by a reduction in photosynthesis per unit leaf area. *Z. aethiopica* NAR changes (a growth parameter, which estimate photosynthetic rate) (Table 3) from different root restriction degree (P and S) and the positive NAR-RGR relationship (Fig. 4a) was found and they are in agreement with previous reports.

Photosynthetic capacity can be limited by leaf thickness [60] as well, which can be estimated at SLA: the higher SLA, the lower leaf thickness. Our results showed that the higher root restriction degree, the higher SLA (Table2). The negative SLA-RGR (Fig. 4c) and SLA-NAR (Fig. 4d) relationships would explain part of the increase in *Z. aethiopica* biomass accumulation and are in agreement with previous results of other ornamental plants [22,31,32].

Changes in the root: shoot ratio are often observed when plants are subjected to various stresses and are the main component of phenotypic plasticity in response to environmental changes [61]. *Z. aethiopica* allometries between roots and shoots (Table 4) showed a higher photo assimilate partition towards shoots (lower β coefficients) in plants cropping in pots or in plants BAP-sprayed. On the other hand, allometries between leaves + petioles and stems and (Table 4) showed lower β coefficients in both P and BAP-sprayed plants, which means that photo assimilates, were

preferentially partitioned towards SAM. *Z. aethiopica* green petioles and pedicels were included because usually showed considerable rates of carbon fixation [62]. Due to photo assimilates partition favored shoots in both P and BAP-sprayed *Z. aethiopica* plants; the higher photo assimilates production, increased root FW (Fig. 1a).

The responses from total plant dry-matter accumulation in *Z. aethiopica* to manipulation of environmental factors, such as temperature and photosynthetic photon flux (PPF), has been reported [63], but the influence of environment on partitioning of dry matter to the tuber only partially. Changes in partitioning with plant development generally restrict the use of harvest indices to crops with a single, readily determined point of harvest. The high correlation between the relative rate of growth (RGR) of the entire plant and the partitioning of the daily increment of dry matter into leaf area development in *Zantedeschia* has been illustrated. Preliminary studies on *Z. aethiopica* suggested that leaf area development is also important to determining tuber growth, but no detailed analysis of dry-matter partitioning or both temperature and PPF relationships has been reported. Funnell et al. [19] suggested that initiation of tuber growth did not require an obligated environmental trigger and that mechanisms of acclimation under different light regimes suggested that tuber growth was principally source limited. Source limitation was expressed either in terms of enhanced inter-sink competition for assimilates, as occurred under the low light regimes, where leaf area development was in direct competition with tuber growth or efficiency of dry-matter accumulation by the leaf area present, as occurred under the high light regimes, where large increases in rhizome growth rate were correlated with increased NAR. Although *Z. aethiopica* plants from seeds and cropping in a greenhouse-amended soil did not develop a visible rhizome (Fig. 2), the higher leaf area or NAR the higher rhizome FW. In the same way, a single BAP spray increases RRGR over controls in potted plants (Table 3).

Roots have a high capacity to sense the physico-chemical parameters of the soil and to adjust their development and performance accordingly, thereby playing an essential role in maintaining the nutritional and development functions of the plant under abiotic stresses [64,65]. Plants are able to detect the presence of their neighbors below ground through the root apical meristem

(RAM), responsible for producing all underground organs [37]. The associated root responses may affect plant performance, but the extent and direction of these responses is heavily debated [66]. Root growth and differentiation in plants has been intimately linked with plant hormones [67].

Cytokinins seem the best candidate for explaining biomass partition changes [68,69]. Endogenous cytokinins are synthesized by roots and are transported to shoot through xylem vessels [70]. O'Hare and Turnbull [71] showed that, an increase in root growth might lead to a corresponding increase in the synthesis of cytokinins. On the other hand, incorporation of cytokinin-producing bacteria into the root zone of lettuce plants has been shown to double the speed of accumulation of shoot biomass at the normal level of water supply [72]. Root-restriction did not alter significantly the levels of total cytokinin bases of the leaves but increased (54-57%) the cytokinin O-glucosides (especially zeatin O-glucosides) [14]. On the other hand, Van Staden et al. [73] indicated that not all the numerous zeatin riboside isomers show the same biological activity. Because the biological activity of all cytokinin-like compounds is not uniform, it normally depends on several structural aspects. The hypothesis that endogenous cytokinins are involved in these responses is supported by the fact that the mentioned physiological changes are similar when ornamentals [21,22,38,39,40,49] and vegetables [13,50,51] were sprayed with exogenous cytokinins. Our results showed positive relationships between RLAE (Fig. 5a), RLA (Fig. 5b), RGR (Fig. 5c), and NAR (Fig. 5d) related to root DW when data from different root restriction degrees and BAP-spray responses were plotted together and partially support this previous hypothesis,

5. CONCLUSION

The large proportion of reduction in pore space occurs within the macro porosity and the rearrangement of soil aggregates increases the tortuosity of pore conductivity. Consequently, compaction restricts plant root growth either by increasing mechanical resistance or by decreasing supply of oxygen, and thereby impedes plant development. We found the same reduced growth pattern in both pot and greenhouse-amended soils but with a significantly higher effect for the last. The more significant growth inhibition was found in rhizome

growth as a result of extremely lower photo assimilate production but with meaningful on propagators. Although biomass accumulation would be related to endogenous cytokinin synthesis, an exogenous BAP spray only significantly increased fresh-dry weight in plants grown in pots filled with a peat-base substrate. Our results showed that a root restriction related to substrate compaction in pots has a lesser impact on *Z. aethiopic* plant growth than a root restriction related to compaction in soils, which cannot be overridden by a single BAP spray regardless of the concentration used.

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COMPETING INTERESTS

Authors have declared that no competing interests exist.

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