

ARTICLE

Methyl jasmonate foliar treatment on growth restriction and leaf anatomy of Begonia ‘Dragon Wing’

Tratamento foliar com metil jasmonato na restrição do crescimento e na anatomia de foliar de Begônia ‘Dragon Wing’

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Abstract: The application of plant growth regulators, primarily gibberellin inhibitors, is the main approach used for controlling the growth of ornamental plants. However, there is a growing interest in alternative products due to the risk of environmental toxicity associated with traditional methods. Methyl jasmonate (MeJa) is a natural substance found in plants and is considered to have low toxicity when used appropriately. Its use as a growth regulator has shown promise for controlling plant growth, but its effects have not been extensively explored in ornamental growth restriction. This study investigated the effects of foliar application of different concentrations of MeJa (0, 50, 100, and 150 μ M) on the growth and leaf anatomy of Begonia ‘Dragon Wing’ Pink and Red. Plant growth parameters were evaluated, and qualitative-quantitative histological analyses of Begonia leaves were conducted. MeJa was efficient in compacting the plants, reducing height in 17.57% and diameter in 8.98% without compromising biomass, root growth, and flowering aspects. The average concentration studied also caused changes in leaf anatomy, increasing the thickness of the abaxial epidermis, reducing mesophyll thickness, the number of calcium oxalate crystals, and the size and number of stomata. The results demonstrated the promising effect of MeJa on controlling the growth of potted ornamental plants.

Keywords: histology, jasmonates, plant growth regulator, potted plant.

Resumo: A aplicação de reguladores de crescimento vegetal, principalmente os produtos inibidores de giberelina, é o principal recurso utilizado para o controle do crescimento de plantas ornamentais, no entanto, é crescente a busca por produtos alternativos devido ao risco de toxicidade ambiental causado. O metil jasmonato (MeJa) é uma substância natural encontrada em plantas e considerado de baixa toxicidade quando utilizado adequadamente, seu uso como regulador de crescimento tem se mostrado promissor para o controle do crescimento de plantas, mas seus efeitos não foram totalmente explorados na restrição do crescimento de ornamentais. O presente trabalho investigou os efeitos da aplicação foliar de diferentes concentrações de MeJa (0, 50, 100 e 150 μ M) no crescimento e na anatomia foliar de Begônia ‘Dragon Wing’ Pink e Red. Foram avaliados parâmetros de crescimento das plantas e conduzidas análises histológicas quali-quantitativas da folha da Begônia. O MeJa foi eficiente em compactar a planta, reduzindo a altura em 17.57% e diâmetro em 8.98% sem comprometer a biomassa, crescimento radicular e aspectos do florescimento. A concentração média estudada também provocou alterações na anatomia foliar, aumentando a espessura da epiderme abaxial, reduzindo a espessura do mesofilo, número de cristais de oxalato de cálcio e o tamanho e o número de estômatos. Os resultados demonstraram o efeito promissor do MeJa no controle de crescimento de plantas ornamentais envasadas.

Palavras-chave: histologia, jasmonatos, planta envasada, regulador de crescimento vegetal.

Introduction

Potted ornamental plants are required to adhere to rigorous marketing standards. Consumers particularly appreciate compact sizes, characterized by reduced plant height and diameter that fill the pot completely (Huylenbroeck and Bhattarai, 2022). To meet these standards, cultural techniques are often employed to restrict growth, such as pruning and the application of chemical growth retardants. However, approaches like pruning are considered outdated for highly productive systems, as they demand skilled labor and incur high costs. Therefore, the use of chemical products is fundamental for controlling the growth of ornamental plants (Rihn et al., 2022).

The most common approach involves the use of plant growth regulators that inhibit gibberellin, a plant hormone responsible for stem elongation (Guleria et al., 2021). Several gibberellin inhibitors are used in floriculture, such as Placbutrazol, Daminozide, and Uniconazole, with effective results in restricting the growth of various ornamental species, such as chrysanthemums, poinsettias, petunias, begonias, carnations, lilies, and gladioli, producing more compact plants with shorter stems and smaller leaves (Aljaser and Anderson, 2021; Collado and Hernández, 2022).

Despite their efficiency in regulating growth, the use of these products has been restricted due to their residual effects on food, soil, and water, as well as their toxicological impact on insects and animals (Zhao et al., 2018; Zhao et al., 2021; Das et al., 2022; Liang et al., 2022).

Jasmonates constitute a group of plant hormones classified within the oxylipin group. Occurring naturally, they are present within plants in the

forms of jasmonic acid (JA) and methyl jasmonate (MeJa), and they govern a variety of physiological processes. These include intercellular signaling pathways, which transmit information between different parts of the plant in response to environmental or physiological stimuli. Additionally, they play a role in plant growth and development by regulating cell division and elongation, as well as by modulating the synthesis and distribution of plant hormones such as auxins and gibberellins. They are also involved in seed germination, root growth, flower and fruit formation, and the senescence process (Kolupaev and Yastreb, 2021).

When used appropriately, methyl jasmonate causes minimal environmental toxicity compared to synthetic gibberellin-inhibiting substances. Research indicates that methyl jasmonate can influence plant growth and development by regulating leaf morphology, enhancing resistance to biotic and abiotic stresses, and influencing the synthesis of secondary metabolites (Karimi et al., 2019; Thakur and Kumar, 2020; Salachna, et al., 2021).

However, studies also reported collateral effects of these molecules in plant development. For example, Li et al. (2018) demonstrated that MeJa application resulted in inhibitory effect on primary root growth and hypocotyl elongation of seedlings, acting as a growth retardant and leading to decreased plant height and biomass. Consequently, its application as a growth regulator holds promise for fostering desirable traits in ornamental plants, such as compactness and branching (Đurić et al., 2023).

Recently, there has been a surge in interest in potted ornamental plants, attributed to their adaptability to limited spaces and enclosed settings (Paiva et al., 2020). Among the species commonly traded in

this format, the *Begonia* genus emerges as notable for its wide array of available species. Nevertheless, owing to its vigorous growth tendencies, strategies are required to maintain the plant's compact form (Sillmann and Mattiuz, 2024).

In this context, this study investigated the effect of MeJa concentrations (0, 50, 100, and 150 μM) as growth inhibitor and their effects in the morphology and leaf anatomy of *Begonia* 'Dragon Wing', aiming to produce compact plants of potted *Begonia*.

Material and Methods

Plant materials and cultivation

We carried out an experiment in the Department of Crop Science, University of São Paulo (ESALQ/USP), Brazil (22°42'30''S, 47°38'00''O, 546 m of altitude), in a greenhouse with 50% shading, from December 2020 to March 2021.

Plants of Dragon Wing *Begonias*, varieties 'Red' and 'Pink', with a commercial standard of 10 cm in height and 4 leaves (Ball Horticultural do Brasil®) were repotted into 2.6 L plastic pots, often used in *Begonia* cultivation, with dimensions of 22 cm in diameter at the top, 13 cm in diameter at the base, and 11.5 cm in height.

Pots were filled with a commercially produced substrate for ornamental plants made of pine bark and Sphagnum peat (Multiplant Grow Mix) with pH 5.8 and density of 252.1 kg cm^{-3} , and plants were placed on concrete benches, positioned 50 cm above ground level, spaced 20 x 20 cm apart, and conducted unpruned.

Pots were supplied with water and nutrients via a drip irrigation system, twice a day at a flow rate of 400 mL s^{-1} . The nutrient solution followed the recommendations for ornamental plants based on Kämpf (2000), including 238 g calcium nitrate (Greenhouse Grade), 368 g potassium nitrate (Paulisol NKS), 180 g MAP (Dripsol MAP) and 0.75 g of micronutrient mix, comprising 2.7% magnesium sulfate, 3% zinc sulfate, 1% copper sulfate, 0.05% sodium molybdate, 4% manganese sulfate, 5.5% borax, and 2% iron sulfate + EDTA (Oligogreen).

The maximum and minimum temperature and humidity measurements were recorded daily by four digital thermohygrometers placed on the benches. The average temperature was 36 °C and the average humidity was 57%.

Methyl Jasmonate application and assessment

The design used was randomized blocks, with four replicates and each block being a bench. We used a factorial design 2x4, with two varieties (*Begonia* 'Dragon Wing' Red and Pink) and four concentrations of MeJa (0, 50, 100, and 150 μM , which correspond to 11.22; 22.44; 33.66 mg L^{-1} , respectively). Each plot was conducted with two plants.

MeJa 95% (Sigma-Aldrich®) was diluted in distilled water and 0.05% Tween20. The solution was applied to the leaves once a week, four times, on alternate weeks. Due to the volatilization of MeJa, its application was conducted inside plastic bags of 10 L, which were kept closed for a period of half an hour to prevent any influence on neighboring plants.

A pre-test was performed to determine the volume of solution needed for complete coverage of the leaves until run-off began, resulting in approximately 10 mL of solution per plant applied using a hand sprayer. The zero-concentration treatment (control) was conducted without application. Treatments started in the third week after transplantation, with all applications carried out in the morning, at 8 am.

Data collection

After 90 days of cultivation, a flexible measuring tape was used to determine plant height (measured from the substrate surface to the apical meristem) and plant diameter (averaged from two perpendicular measurements of diameter in top view). The number of flowers at the bud and opening stages, as well as the number of leaves, was evaluated. Leaf

area was estimated using ImageJ® software, with all leaves detached at the base of the petiole of each plant and laid open on a white background for image capture and analysis.

The roots were separated, and cleaned, and their length was measured using a ruler. All plant parts were separated to determine the fresh masses of the shoot, flowers, and roots. To measure the dry weight, the materials were placed in paper bags and dried in a forced air circulation oven set at 70 °C until a constant mass was reached.

Based on the positive responses of MeJa on plant growth, we collected leaves from the medium concentration tested (100 μM) and the control plants of *Begonia* 'Dragon wing Red' for histological evaluation. Three plants from each treatment were randomly selected, where six fully expanded leaves were collected from the median portion of the plant, starting from the 3rd node.

The anatomical analyses were conducted according to Marques and Nuevo (2022). Samples of 1 cm were taken from median part of the leaves and fixed in Karnovsky solution (Karnovsky, 1965). Thus, the samples were dehydrated in ethanolic series (30%, 50%, 70%, 90%, and 100%), during this process the air was removed from the samples with a vacuum pump. After this, the samples were embedded in Technovit® resin according to the manufacturer's recommendation. The polymerized blocks formed were cut on a rotary microtome, with the sections arranged on a glass slide and stained with toluidine blue.

In total, nine samples were sectioned from each treatment, from which 60 sections of 7 μm each were extracted. Sixteen random sections were chosen from which three sectors of each cut were analyzed, totaling 144 images per treatment that were analyzed under a light microscope (Zeiss, Axionscope), with a video camera attached to the equipment.

The leaf morphometrical parameters (abaxial epidermis, adaxial epidermis, palisade parenchyma, spongy parenchyma, mesophyll, and total tissue thickness) were measured with two repetitions per image, using ImageJ® software.

In addition, the fixed samples were bleached by ethanolic series (30%, 50%, 70%, 90%) to remove chlorophyll and then arranged the slides in ethanol to observe the adaxial and abaxial epidermis. A total of 15 images were made on each side of the leaf, from 3 different repetitions. Analyses under polarized light to detect calcium oxalate crystals were also conducted on these samples. The area of adaxial epidermal cells, number of stomata in the cluster, width, length of stomata, and cluster area were measured in ImageJ® software.

Statistical analysis

Data were statistically evaluated by performing the F-test of the analysis of variance, Tukey's test for comparison of means, and regression adjustment when necessary, using PROC MIXED of SAS® 9.4 software (SAS Institute, 2013).

Results and Discussion

Both varieties exhibited similar responses to methyl jasmonate (MeJa) treatment, as there was no significant interaction between the studied doses (0, 50, 100, and 150 μM) and the varieties (Red and Pink). This finding is crucial as it suggests that both genotypes responded similarly to increasing concentrations. Consequently, standardizing the use of MeJa for both varieties is feasible.

In comparing the studied concentrations, a significant difference was observed between the means of plant height and diameter. The quadratic regression model provided a better fit for both factors. However, concerning plant height, all MeJa treatments exhibited a similar decrease compared to the control, averaging 17.57%, with an average height of 34.9 cm (Fig. 1A). Regarding plant diameter, only the highest concentration of MeJa showed a significant difference from the control, resulting in a diameter of 41.6 cm, representing a reduction of 8.98% (Fig. 1B).

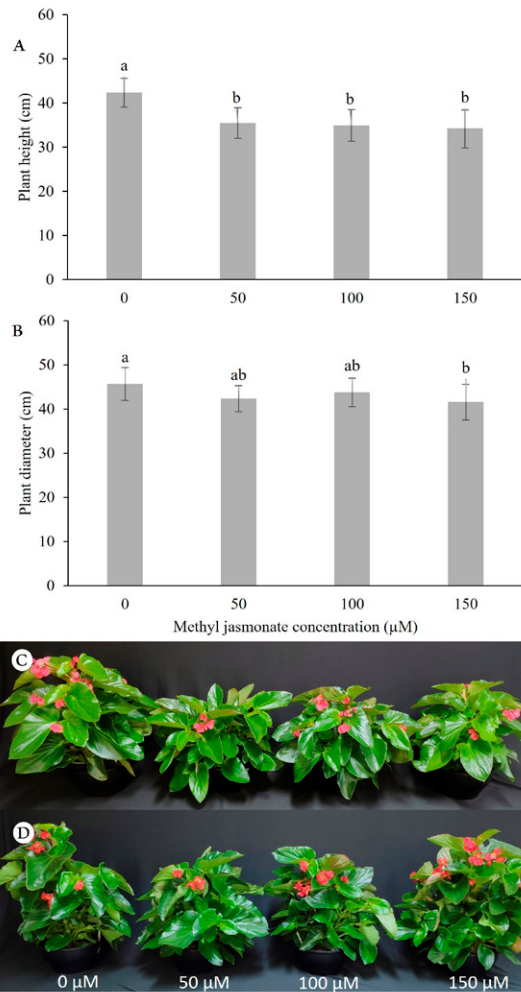


Fig. 1. Plant height (A) and plant diameter (B), in cm, of Dragon Wing Begonia plants following spray treatments with different Methyl Jasmonate concentrations (μM) after 90 days of cultivation. Statistically different ($p < 0.05$) values are denoted by lowercase letters according to Tukey's test and each bar shows the mean \pm SD ($n = 8$). 56-week-old Pink Dragon Wing Begonia plants (C) and 56-week-old Red Dragon Wing Begonia plants (D) treated with spray solution of Methyl Jasmonate concentrations at 0, 50, 100 and 150 μM .

Generally, jasmonates collaborate with other hormones to induce stress tolerance, eliciting physiological responses such as activating the antioxidant system, accumulating amino acids, and regulating stomatal closure. At the molecular level, they influence gene expression and interact with other hormones. Consequently, jasmonates play a role

in regulating plant growth by prioritizing the functioning of secondary metabolism (Wang et al., 2020). This control mechanism prioritizes the defense system over plant growth, consequently leading to reduced plant height, as observed in the present study (Fig. 1A).

In sunflower, MeJa significantly reduced plant height and biomass and in soybean the same authors observed a 17% reduction in plant height (Li et al., 2018), a value similar to that found in the present study; however, this reduction was achieved with a high concentration of MeJa (1 mM), a concentration 20 times higher than that studied by us. The growth of Begonia plants was reduced even at the lowest dose (50 μM) demonstrating the high susceptibility of Begonia to the treatment (Fig. 1A).

Many studies have demonstrated the efficacy of plant growth regulators in reducing the size of potted ornamental plants, with particular emphasis on gibberellin inhibitors (Shin et al., 2020; Shi et al., 2021). In this study, we utilized MeJa, a phytohormone extracted from plant sources, to investigate its potential for compacting the size of an ornamental plant known for its vigorous growth.

The treatment showed promising results in reducing growth, resulting in decreases in plant height and diameter (Fig. 1, A and B), thus Begonia plants consistently displayed compact, rounded pot shapes across all MeJa treatments and exhibited a more uniform and compact growth habit compared to control. In particular, the control treatment demonstrated poorer performance compared to the MeJa treatments, leading to plants with reduced market value (Fig. 1, C, and D).

When applying MeJa on plants, some authors have reported its beneficial effects on enhancing plant resistance to stress. In ornamental plants, its impact is notable in post-harvest flower maintenance due to its antifungal properties, ability to combat oxidative stress, and promotion of higher concentrations of floral essences and essential oils (Chen et al., 2021). However, various studies have also noted that while exogenous jasmonate application enhances resistance to both biotic and abiotic stressors, it can lead to reduced growth a drawback in crop plants (Heijari et al., 2005; Salachna et al., 2020).

In our study, we are investigating the impact of MeJa on growth restriction as a means to align with market standards for ornamental plants. However, we have not disregarded its potential effectiveness in mitigating begonia diseases.

Despite the reduction in plant height and diameter, the MeJa treatments did not affect biomass, number of leaves, leaf area, or root length, this demonstrates that in Begonia, such treatment does not affect the plant's architecture but rather its stature, which is crucial for pot quality. Additionally, there were no changes in inflorescences, as evidenced by the consistent number of flowers and buds and the dry mass of flowers (Table 1).

Usually, the observed results vary depending on the species, but concentrations lower than 1000 μM are considered low and do not significantly affect plant growth (Moreira et al., 2012; Li et al., 2018). However, studies by Maciejewska and Kopcewicz (2002) and Salachna et al. (2020) reported effects on the flowering of *Pharbitis nil* L. and amaryllis, respectively, at these lower concentrations. In their research, MeJa delayed flowering and reduced the number of inflorescences, contrary to the findings of this study, where such changes were not observed.

Table 1. Morphological traits of Dragon Wing Begonia plants treated with spray solution of Methyl Jasmonate concentrations at 0, 50, 100 and 150 μM .

Morphological traits	Methyl Jasmonate Treatment				C.V.
	0	50	100	150	
Number of flowers ^{ns}	14.1	9.2	7.0	13.2	37.6
Number of buds ^{ns}	23.1	18.0	19.6	19.3	17.4
Number of leaves ^{ns}	218.3	178.0	173.5	173.7	10.3
Leaf area (cm ²) ^{ns}	70.1	64.6	65.2	62.6	14.1
Shoot dry mass (g) ^{ns}	88.6	81.5	86.6	73.0	21.5
Flower dry mass (g) ^{ns}	5.1	4.6	4.8	4.2	31.9
Root dry mass (g) ^{ns}	4.3	3.9	3.8	3.7	22.3
Root length (cm) ^{ns}	20.9	21.6	20.0	21.7	13.7

Statistically different ($p < 0.05$) values are denoted by lowercase letters within rows according to Tukey's test ($n=8$ for number of flowers, buds, and leaves; $n=4$ for the other variables). ns p -value > 0.05 ; * p -value < 0.05 . "C.V." = coefficient of variation.

There are few studies comprising the anatomical analysis of leaves treated with MeJa, but it is possible that there is an acclimatization in leaf anatomy as a function of the application of the plant hormone, which may differ between species and different concentrations (Li et al., 2018).

In this study, the concentration of 100 μM modified the leaf anatomy, due to the compaction of the size of the leaf mesophyll, by the reduction of the palisade and spongy parenchyma. The changes observed in the palisade parenchyma were caused by the decrease in cell length, while the change in the spongy parenchyma promotes the decrease in intercellular space (Fig. 2). This may be related to the increase in abaxial epidermal cell height of about 9%, which may promote biomechanical pressure to compress the spongy parenchyma (Table 2).

The MeJa treatment provided a decrease in leaf blade thickness, there was a reduction of 11.60% in palisade parenchyma, 14.67% in spongy parenchyma, and 10.47% (31.78 μm) in mesophyll. It also altered the size of stomata, reducing the length of stomata by 15% and reduced the cluster area by 25%, in addition to reducing the average number of stomata

by 33% (Table 2). As well, it was observed the presence of druse-type calcium oxalate crystals in spongy parenchyma cells, these crystals were observed in smaller quantities in MeJa-treated leaves (Fig. 2).

Li et al. (2018) reported in a study with MeJa changes in the thickness of the epidermis and cuticle, observed a decrease in soybean and sunflower and a thickening in tomato, showing that the effects may be different depending on the species. Leaf thickness is associated with the ecological performance of plants, as it is linked to light absorption and CO_2 diffusion, there is a relationship between leaf thickness and photosynthesis, for example, compaction of the palisade parenchyma can result in plants that are more resistant to pathogens, but with lower photosynthetic efficiency and lower growth (Silva et al., 2005).

This feature of mesophyll compaction may be related to the lower growth of plants treated with MeJa, however, other studies also infer this decrease to the crosstalk between jasmonates and gibberellin, due to the signaling of jasmonates antagonizing gibberellin biosynthesis (Zhang et al., 2021; Panda et al., 2022).

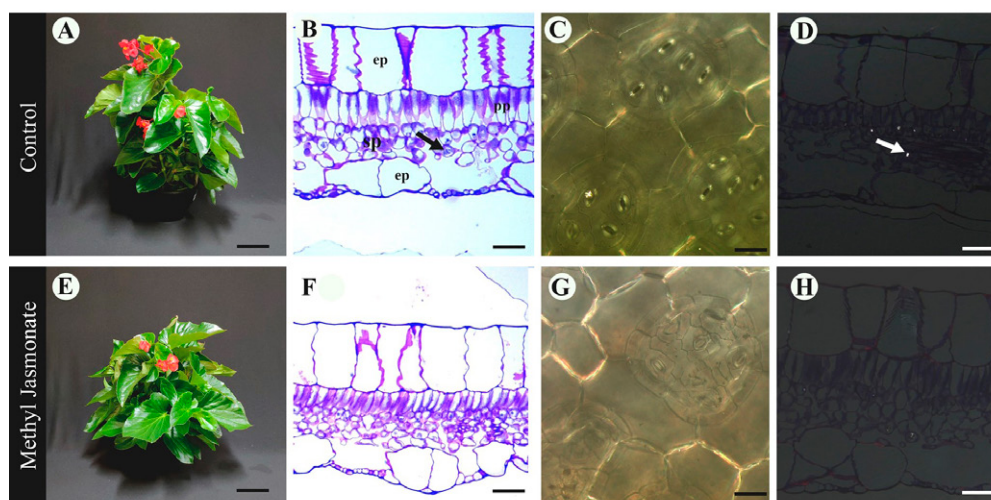


Fig. 2. 56-week-old Red Begonia ‘Dragon Wing’ plant, control (a) and treated with MeJa 100 μM (e). Cross-sections of the leaf lamina stained with toluidine blue (b, f, d, h) and images using polarized light (d, h). Micrographs of dehydrated leaf (c, g). Control (a-d) and treatment with MeJa (e-h). ep, epidermis; pp, palisade parenchyma; sp, spongy parenchyma; calcium oxalate crystals (arrow) in spongy parenchyma cells. Bars: (a, e): 7 cm; (b, d, f, h): 100 μm ; (c, g): 50 μm .

Table 2. Anatomical traits of Dragon Wing Begonia leaves treated with exogenous MeJa.

Anatomical Traits	Control	MeJa Treatment	C.V.
Total leaf thickness (μm) ^{ns}	471.8	462.1	1.15%
Adaxial cuticle thickness (μm) ^{ns}	176.9	172.2	34.97%
Mesophyll thickness (μm)*	194.5 ^a	174.1 ^b	3.67%
Palisade parenchyma thickness (μm)*	74.7 ^a	66.0 ^b	14.04%
Spongy parenchyma thickness (μm)*	114.4 ^a	97.6 ^b	5.91%
Abaxial cuticle thickness (μm)*	96.2 ^b	104.4 ^a	9.76%
Stomata length (μm)*	33.3 ^a	31.6 ^{ab}	15.15 %
Stomata width (μm)*	23.6 ^a	19.9 ^b	15.18 %
Stomata area (μm^2)*	54988 ^a	41139 ^b	28.06 %
Stomata number/cluster*	8.8 ^a	5.9 ^b	26.65 %

Statistically different ($p < 0.05$) values are denoted by lowercase letters within rows according to Tukey’s test ($n=96$). ns p -value > 0.05 ; * p -value < 0.05 . “C.V.” = coefficient of variation.

The effect of plant hormones on plant anatomy, such as gibberellin, was reported in other studies, showing that they can also modify the pattern of stomata, the exogenous application of jasmonates can inhibit the development of stomata, decreasing the density and number of stomata and inducing stomatal closure and can infer in the decrease of cluster size, corroborating with the results found in this study (Han et al., 2018; Li et al., 2018).

In addition, calcium oxalate crystals were observed in smaller quantities in the leaves treated with MeJa, according to the study by Volk et al. (2002), the shape of the crystal is linked to its function in the plant, drusa crystals are related to calcium regulation and are dependent on its concentration in the plant, the deficiency of this element accompanied by the active growth of the plant causes the decrease and even the disappearance of the crystals.

The lower formation of crystals in the treatment with MeJa may be related to the interaction between jasmonates and calcium, Aslam et al. (2021) showed that the exogenous application of jasmonates infers an increase in the concentration of Ca^{2+} in the cytosol, releasing it from internal cell reserves. Such characteristic may have contributed to the lower observation of crystals in the treatment with MeJa in this study.

Although the genus *Begonia* is one of the largest and most diverse collections of species, characterized by a wide variety of leaf shapes and colors, there is a notable scarcity of studies focusing on its morphological characteristics and leaf anatomy (Sillmann and Mattiuz, 2024). In our experiment, Dragon Wing *Begonia* demonstrated vigorous growth and great rusticity, as evidenced by both morphological and anatomical assessments. These findings suggest its significant potential for commercialization, owing to its ornamental appeal and ease of cultivation.

Conclusions

Foliar treatment with MeJa emerged as a promising method for compacting potted *Begonia* Dragon Wing 'Pink' and 'Red'. Even at low concentrations (50, 100, and 150 μ M), MeJa effectively inhibited plant growth, mainly by reducing the plant's height, resulting in specimens ideal for the market, with ornamental features highly valued by consumers. Furthermore, MeJa at 100 μ M modified the leaf anatomy by decreasing leaf thickness and the number of stomata and calcium oxalate crystals.

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Author contributions

CFMM: conceptualization, validation, methodology, resources, writing- reviewing and editing, supervision. **TAS:** conceptualization, methodology, investigation, data curation, writing- reviewing and editing. **JPRM:** methodology, validation, writing- reviewing and editing, supervision. **SMSP:** data curation, software, validation.

Declaration of interest statement

The authors reported no potential conflict of interest.

Data Availability Statement

Data will be available on request.

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