




Biomass accumulation of *Schlumbergera truncata* (Haw.) Moran (Thanksgiving cactus) grown under high pot density

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ABSTRACT

The growth of most pot-grown succulents offered by the ornamental industry is limited mainly by water, nutrients, photoperiod, and temperature manipulation, while other decisions, such as: plant density at pot cropping are often based on the grower's experience. In the present study, to optimize the biomass accumulation of *Schlumbergera truncata* under high pot density, we performed an experimental design that included different numbers of initial phylloclades and spraying or not with the synthetic cytokinin 6-benzylaminopurine (BAP). The highest biomass accumulation on a fresh weight basis and highest stem area expansion were recorded in pots with five initial phylloclades and BAP-sprayed plants. The decrease in individual biomass accumulation and the expansion of stem area were related to an increase in pot density. Since shading effect can be discarded, responses to photo-assimilate uptake and distribution more associated with mechanical constraints on pot roots rather than with a competition between individual roots. Our results suggest that, when *Schlumbergera truncata* is grown in pots, the number of initial phylloclades may be higher than the usually recommended number per pot.

Keywords: *cactus growth, cytokinin, pot cropping, space competition.*

INTRODUCTION

The global demand for flowering plants is increasing along with the growing for novelty from the floriculture industry. In this context, epiphytic cacti have great economic importance (influence) as potted plants in the horticultural trade worldwide (Sriskandarajah *et al.*, 2007), and the Thanksgiving cactus (*Schlumbergera truncata* (Haw.) Moran) has become a popular ornamental plant due to its beautiful flowers, wide flower color range, unusual plant form, and product diversification by growers.

All species of cactus family (with extremely rare exceptions) exhibit Crassulacean acid metabolism (CAM), a carbon-concentrating photosynthetic pathway that allows plants to acquire CO₂. However, CAM is energetically costly and the relative growth rate (RGR) of species with CAM is usually lower than that of plants with a C₃ biochemical cycle (Shameer *et al.*, 2018). Additionally, this cactus, is native to the rainforest of the peripheral mountains

of southeastern Brazil, north of Rio de Janeiro (Boyle, 2007; Gonzaga et al., 2019), is environmentally adapted to relative low irradiances (Nobel and Bobich, 2002).

Although cacti can grow in very dense stands, experiments in pots with cactus plants such as the columnar Cardon (*Pachycereus pringlei*) and the saguaro (*Carnegiea gigantea*) have shown that increases in population density reduce their height and dry weight (Bacilio et al., 2011). Regarding *Schlumbergera truncata*, little is known about its cultural requirements. Although this cactus does not have the typical requirements of most succulents, experimental work has been concentrated mainly on chemical issues (Araújo Rodrigues and Soares Queires, 2015; Tavares et al., 2016), photoperiod, and temperature manipulation (Nobel and Bobich, 2002), while other recommendations such as plant density during pot cropping are often based on the grower's experience. In general, to compensate for the low growth rate of each cactus cutting, *Schlumbergera truncata* growers include many phylloclades in each pot. The number of segments planted per pot varies with the cultivar and pot size and ranges between one to five segments per pot (Di Benedetto, personal observation).

Tools to improve yield, such as spraying with the exogenous synthetic cytokinin 6-benzylaminopurine (BAP), have been recently suggested for the ornamental *Mammillaria elongata* subsp. *Echinaria* grown in pots (Lozano-Miglioli et al., 2019). This is an agreement with was reported by Boyle (1992), who found that, in both *Schlumbergera truncata* and *Rhipsalidopsis Gaertneri* (a related epiphytic cactus), the number of new phylloclades increases linearly in response to increased BAP concentrations. However, studies focusing on the growth and development of *Schlumbergera truncata* are not frequent (Da Silva et al., 2017) and tools for increasing the grower's management are needed.

Based on all the above, and on the hypothesis that crop yield would be optimized with a suitable pot density and the use of a BAP spray, this work aimed was to evaluate the effect of a single BAP spray and a different number of initial phylloclades per pot on the vegetative growth of the cactus *Schlumbergera truncata*.

MATERIALS AND METHODS

Plant material, treatments, and experiments

The experiment was conducted in a greenhouse facility placed at the campus of the Faculty of Agronomy of the University of Buenos Aires, Argentina (34° 35' 59"S, 58° 22' 23"W) from November 12th, 2018 to June 14th, 2019.

Different numbers of rooted phylloclades (2.437 ± 0.241 g cladode⁻¹ fresh weight) of *Schlumbergera truncata* (How.) Moran was transplanted into 1.5-L plastic pots (1, 2, 3, 4, or 5 per pot). Pots were filled with a 2:2:1 (v/v) mix of *Sphagnum maguellanicum* peat, river waste, and, perlite. Plants were watered daily to saturation and fertilized weekly with N, P, K and Ca fertilizer added to the irrigation water (50 mg L⁻¹ N) (2:1:2:2 N: P: K: Ca). The plants were arranged at a density of six plants m⁻².

Phylloclades were sprayed with different BAP (6-benzylaminopurine; SIGMA EC 214-927-5) (Sigma-Aldrich Co., St. Louis, MO, USA) solutions (0, 5, 50, 100, and 200 mg L⁻¹) two weeks after transplant. BAP was previously diluted in alcohol 80%.

During the experiment, meteorological data were recorded with a HOBO sensor (H08-004-02) (Onset Computer Corporation, MA, USA) connected to a HOBO H8 data logger. The mean air temperatures ranged between 23.03 and 25.77°C, whereas the global solar radiation ranged between 5.45 and 7.23 mol photons m⁻² day⁻¹.

Sample and growth evaluations

For destructive measurements, ten plants per treatment and sampling date were randomly chosen at the beginning of the experiment (transplant stage) and 30, 60, 90, 120, 150, 180, and 210 days after transplant. Roots were washed and root and shoot fresh weights (FW) were recorded. Dry weights (DW) were recorded after drying roots and shoots to constant weight at 80°C for 96 hours. The number of cladodes was also recorded, and each phylloclade area was determined using the ImageJ® (Image Processing and Analysis in Java) software.

The growth parameters used in this work, i.e. the rate of phylloclade appearance (RPA), the rate of stem area expansion (RSAE), the specific phylloclade area (SPA), the relative growth rate (RGR), the net assimilation rate (NAR), the root/shoot ratio, the stem area partitioning (SAP), the allometries between root and shoots, and the stem area index (SAI), were determined as previously described (Di Benedetto and Tognetti, 2016).

Statistical analysis

Data were subjected to a two-way ANOVA for a completely randomized design after checking ANOVA assumptions, including normality of variances (Shapiro-Wilk's test) and homogeneity of variances (Levene's test). Means were compared by Tukey's test ($P < 0.05$). When applicable, Fisher's LSD-test ($P < 0.05$) was applied to determine the direction of the differences among treatment means. Slopes from straight-line regressions of RPA, RGR, NAR, SAP, and allometric values were tested using the SMATR package.

RESULTS

Fresh weight accumulation

When the number of rooted phylloclades of *Schlumbergera truncata* placed in each pot increased, the FW accumulated in individual plants did not change until three initial phylloclades per pot were harvested at the end of the experiment. A higher number of plants per pot decreased individual FW. When a BAP spray was applied, higher FW accumulation was observed and the decrease in individual size was evident only when five plants were placed in each pot (Figure 1A). However, as the number of plants increased, the FW per pot was higher, with smaller differences between controls and BAP-sprayed plants (Figure 1B).

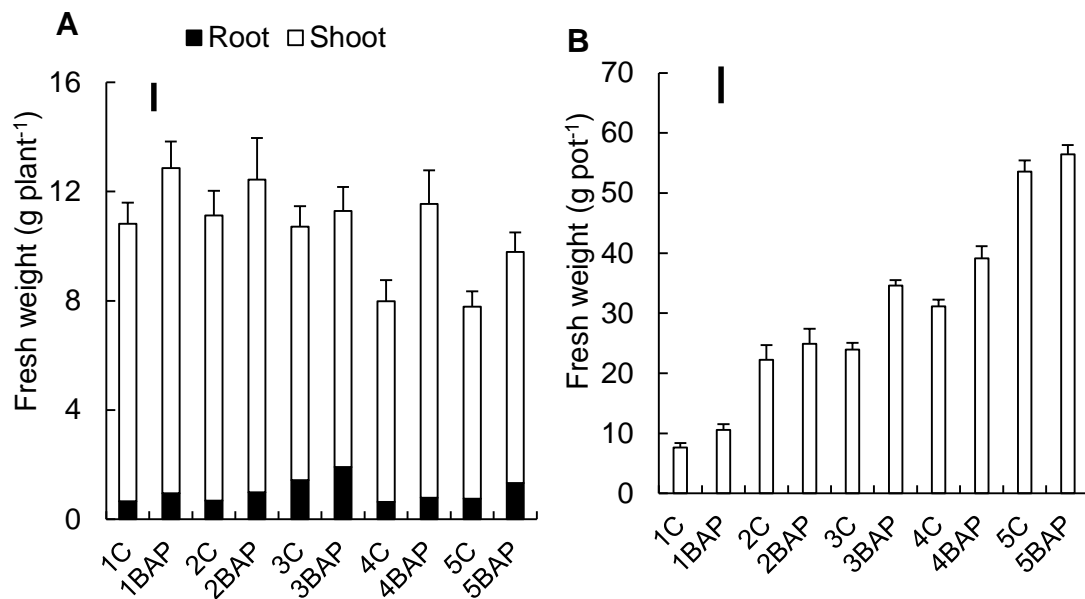


Figure 1. Biomass accumulation on a fresh weight basis in roots and shoots at the end of the experiment in plants of *Schlumbergera truncata* sprayed with or without 100 mg L⁻¹ BAP in pots with 1 to 5 initial phylloclades pot⁻¹ (A). Fresh weight per pot for the same treatments. Vertical lines indicate the least significant differences (Fisher's LSD) among treatments.

Stem area expansion

Near to FW, the phylloclade area per pot increased as the number of initial *Schlumbergera truncata* phylloclades increased (Figure 2A). At the end of the experiment, we found some differences in total stem area (Figure 2B) or individual phylloclade area (Figure 2C) between one and five initial cuttings per pot. The BAP spray increased stem area expansion in both traits to a different extent.

At the end of the experiment, the SAI in pots with one or two plants was low and significantly higher when three to four plants were included in each pot. The BAP spray increased SAI in pots with three, four, or five plants (Figure 3). However, maximum SAI values were low.

As the initial cutting number increased, RPA and RSAE on an FW basis decreased. The single BAP spray at the beginning of the experiment increased both RPA and RSAE (Table 1).

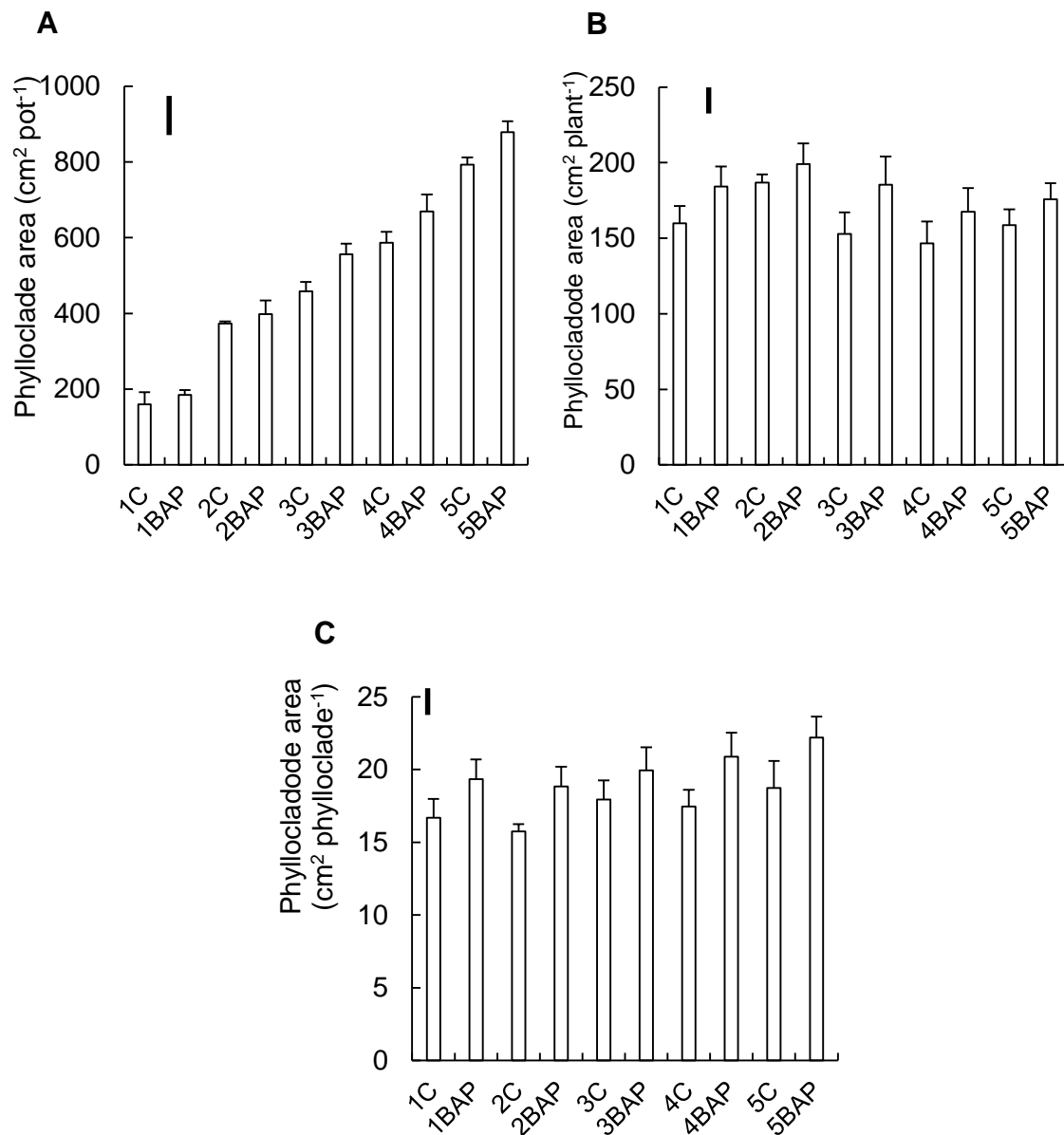


Figure 2. Changes in phylloclade area per pot (A), per plant (B), and phylloclade (C) at the end of the experiment in plants of *Schlumbergera truncata* sprayed with or without 100 mg L^{-1} BAP in pots with 1 to 5 initial phylloclades pot^{-1} .

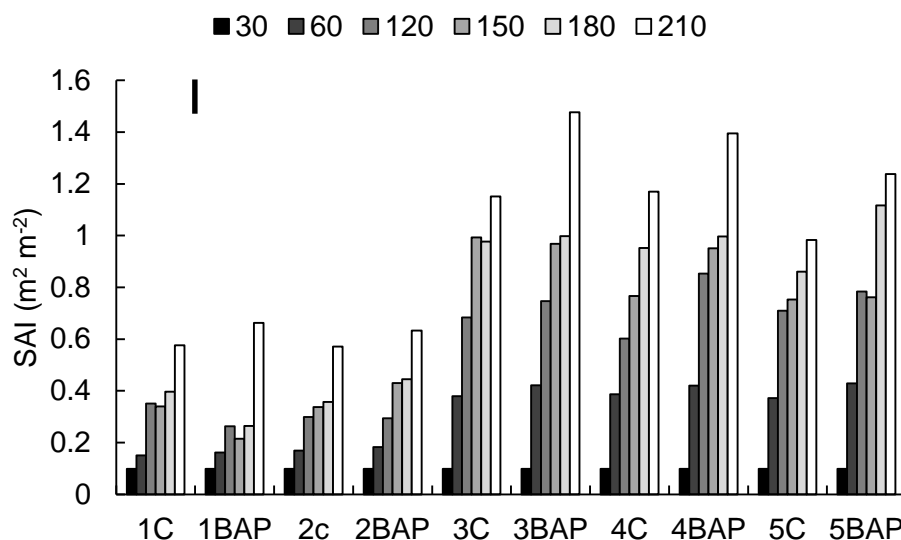


Figure 3. Changes in stem area index (SAI) during the experiment in the plants of *Schlumbergera truncata* sprayed with or without 100 mg L⁻¹ BAP in pots with one to five initial phylloclade pot⁻¹.

Table 1. The changes in plants growths parameters related to the expansion area of photosynthetic, at the end of the experiment in the plants of *Schlumbergera truncata* sprayed with or without 100 mg L⁻¹ BAP on pots with one to five initial phylloclade pot⁻¹. Different lower case letters indicate significant differences ($P < 0.05$) among treatments.

| | RPA (phylloclades day ⁻¹) | RSAE (cm ² cm ⁻² day ⁻¹) |
|------|--|---|
| 1C | 0.0470c | 0.0104ab |
| 1BAP | 0.0495a | 0.0111a |
| 2C | 0.0419c | 0.0098b |
| 2BAP | 0.0451b | 0.0096b |
| 3C | 0.0292f | 0.0073d |
| 3BAP | 0.0354d | 0.0088b |
| 4C | 0.0236f | 0.0097a |
| 4BAP | 0.0307e | 0.0111a |
| 5C | 0.0219f | 0.0078c |
| 5BAP | 0.0431b | 0.0090b |

Dry weight accumulation

Growth parameters that objectively quantify biomass accumulation on a DW basis, such as RGR (shoots + roots), RGR_{Roots}, and NAR, decreased according to an increase in the number of plants per pot, with the highest values observed in BAP-sprayed plants. At the same time, an inverse response was observed in SPA (Table 2).

Table 2. Changes on plants growths parameters are related to the biomass accumulation, at the end of the experiment in plants of *Schlumbergera truncata* sprayed with or without 100 mg L⁻¹ BAP in pots with one to five initial cuttings pot⁻¹. Different lower case letters indicate significant differences (P < 0.05) among treatments. SPA were performed on a dry weight base.

| | RGR (g g ⁻¹ day ⁻¹) | RGR_{Roots} (g g ⁻¹ day ⁻¹) | NAR (g cm ⁻² day ⁻¹) x 10 ⁻⁵ | SPA (cm ² cm ⁻²) |
|------|--|--|---|---|
| 1C | 0.0084c | 0.0146c | 5.30d | 298.07d |
| 1BAP | 0.0103a | 0.0168a | 6.46a | 250.39e |
| 2C | 0.0088c | 0.0147c | 5.03d | 279.01d |
| 2BAP | 0.0109a | 0.0155b | 5.96b | 264.99e |
| 3C | 0.0084c | 0.0129d | 4.68f | 320.25c |
| 3BAP | 0.0096b | 0.0142c | 5.79c | 282.47d |
| 4C | 0.0070d | 0.0104f | 4.00h | 354.66c |
| 4BAP | 0.0087c | 0.0131d | 4.98e | 345.39c |
| 5C | 0.0072d | 0.0088g | 4.32g | 532.66a |
| 5BAP | 0.0076d | 0.0112e | 4.93e | 426.94b |

Photo assimilates partitioning

In control plants, the root/shoot ratio at the end of the experiment increased as the number of cuttings per pot increased. The same pattern was found in BAP-sprayed plants, but with a significantly lower root/shoot ratio than control plants. The phylloclade area partition (PAP) and the β coefficient from the root/shoot allometries showed a higher partition to shoots (Table 3).

Table 3. Changes in plant growth parameters related to the photoassimilate partitioning in plants of *Schlumbergera Truncata* sprayed with or without 100 mg L⁻¹ BAP in pots with one to five initial cutting pot⁻¹. Different lower case letters indicate significant differences (P < 0.05) among treatments.

| | Root/Shoot ratio | SAP (cm ² day ⁻¹ /g day ⁻¹) | β |
|------|-------------------------|---|---------------------------|
| 1C | 0.183 | 179.54c | 1.164a |
| 1BAP | 0.130 | 172.87c | 0.803e |
| 2C | 0.202 | 244.72a | 0.990d |
| 2BAP | 0.156 | 192.87b | 0.747f |
| 3C | 0.168 | 168.98c | 0.836e |
| 3BAP | 0.131 | 178.48c | 0.766f |
| 4C | 0.325 | 192.69b | 0.770f |
| 4BAP | 0.161 | 186.31b | 0.992d |
| 5C | 0.372 | 147.05d | 1.035c |
| 5BAP | 0.275 | 139.30e | 1.105b |

Relationships among growth parameters

RPA (Figure 4A), RSAE (Figure 4B), NAR (Figure 4C), and RGR showed a direct relationship. In contrast, SPA (Figure 4D), SAP (Figure 4E), β coefficient (Figure 4F), and RGR showed an inverse relationship.

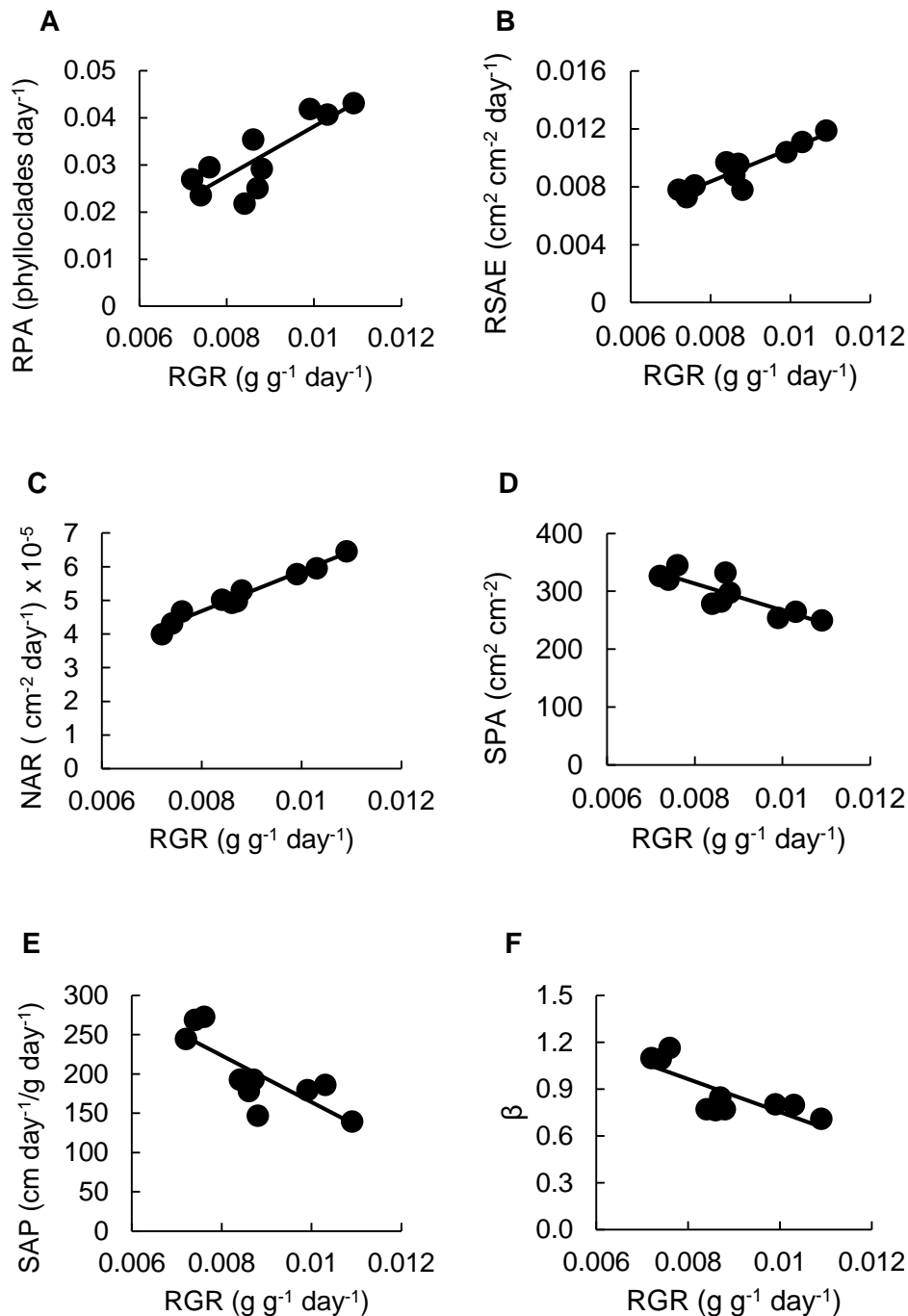


Figure 4. Relationships between the rate of phyllode appearance (RPA) (A), the rate of stem area expansion (RSAE) (B), the net assimilation rate (NAR) (C), the specific phyllode area (SPA) (D), the stem area partitioning (SAP) (E), the β coefficient root: shoot allometries (F) and the relative growth rate (RGR) in plants of *Schlumbergera truncata* sprayed with or without 100 mg L⁻¹ BAP in pots with 1 to 5 initial phyllode pot⁻¹. The straight-line regressions were, RPA = 5.28 RGR - 0.016 ($r^2 = 0.687$; $P < 0.001$); RSAE = 1.14 RGR - 0.0007 ($r^2 = 0.834$; $P < 0.001$); NAR =

594.47 RGR - 0.075 ($r^2 = 0.967$; $P < 0.001$); SPA = -23138 RGR + 498.63 ($r^2 = 0.712$; $P < 0.001$); SAP = -29786 RGR + 461.80 ($r^2 = 0.631$; $P < 0.001$); $\beta = -105.50$ RGR + 1.81 ($r^2 = 0.617$; $P < 0.001$);

DISCUSSION

After seven months of growth, control plants increased total biomass on an FW basis (Figure 1B) and leaf area (Figure 2A) as the number of initial phylloclades per pot increased, with the highest values in pots with five initial phylloclades. When a single BAP spray of 100 mg L⁻¹ was applied at the beginning of the experiment, a significant increase in both FW and leaf area per pot was founded, in agreement with previous reports on vegetables (Di Benedetto *et al.*, 2020b) and ornamental plants (Di Benedetto *et al.*, 2020a), including cacti (Boyle, 1992, Lozano-Miglioli *et al.*, 2019), grown in pots. However, to optimized *Schlumbergera truncata* management in commercial environments, our experimental design gave a wide approach to the intraspecific competition processes established between different cuttings grown in potted systems, which compete for light, space, water, and nutrients. An increase in the number of initial phylloclades and growth rate through a BAP spray determined ten different plant densities through the experiment.

Bacilio *et al.* (2011) showed that an increase in plant density in cactus plants such as the columnar Cardon (*Pachycereus pringlei*) and the saguaro (*Carnegiea gigantea*) grown in pots reduces height and DW, in agreement with our data in *Schlumbergera truncata*, which showed a lower FW (Figure 1B) and stem area per plant (Figure 2B). Biomass accumulation and stem area expansion would be limited at plant level by light, space, or mineral resources. In the present study, the BAP spray increased stem area per phylloclade, which in turn increased light interception and plant requirements for water, and mineral nutrients. However, non-limited water and nutrient supply were guaranteed by the fertigation system used.

Because of the absence of leaves, most cacti, including *Schlumbergera truncata*, fix carbon with their green photosynthetic stems. Analysis of growth parameters related to stem expansion indicated that plant light interception related to RPA and RSE (Table 1) decreased as the number of initial phylloclades increased, even if an early BAP spray allowed obtaining higher RPA and RSE from each initial phylloclade density tested. Although SAI increased through the experiment in reciprocity to biomass accumulation per pot, the SAI values at the end of the experiment were relatively low and in agreement with that observed in other cacti in field environments (De Amorin *et al.*, 2015; Da Silva *et al.*, 2016) as to limit plant growth.

Biomass accumulation on a DW basis (data not shown) showed the same pattern response as stem area, and changes related to increase the competition between different plants could be estimated through RGR (Hüber *et al.*, 2018). In this way, our RGR data (Table 1) changed in agreement with FW accumulation (Figure 1) and stem area expansion (Figure 2). In cacti, RGR is largely controlled by both NAR (Delgado Sánchez *et al.*, 2013; Lozano-Miglioli *et al.*, 2019). Our results showed that the response changes in our experiment were related to changes in NAR (Table 1).

Stem biomass accumulation is finally supporting by changes in photo-assimilate partitioning. Both SAP and the β coefficient from the root/shoot allometries indicate a higher photo-assimilate partitioning to stems as the number of initial phylloclades increased and with the BAP spray. This last result is in agreement with previous reports on other vegetables (Di Benedetto *et al.*, 2020b) and ornamentals (Di Benedetto *et al.*, 2020a), including cacti (Lozano-Miglioli *et al.*, 2019).

Root system extension and root volume occupation can be estimating through RGR_{Root} . The results shown in Table 2 show significant changes in root DW accumulation between treatments, which indicate that a decrease in RGR_{Roots} would be a response to a greater extension to the usual root restriction effect developed in the presence of pot resistance (Hassan *et al.*, 2019, 2020; Di Benedetto *et al.*, 2020a) rather than to a root competition with the other neighboring roots. Additionally, the results have shown in Table 3 shows an increase in the root/shoot ratio in pots according to an increase in the number of initial phylloclades or BAP applications.

Most *Schlumbergera Truncata* growth parameters related to stem area expansion, photo-assimilate acquisition, and photo-assimilate partitioning showed a high correlation with RGR (Figure 4). On the other hand, these results are in agreement with previous reports from our laboratory in ornamentals, vegetables, and cacti (Di Benedetto *et al.*, a, b; Lozano-Miglioli *et al.*, 2019), which indicated a close relationship between the root system size and shoot biomass accumulation, mainly related to the effective endogenous level of cytokinin at the shoot apical meristem. In this regard, Sriskandarajah *et al.* (2006) showed that the total of content of isopentenyl-type cytokinins in greenhouse-grown leaves of the cactus *Rhipsalidopsis Gaertneri* was more than twice the amount found in leaves of *Schlumbergera Truncata*. These authors indicated that exogenous BAP supplies were needed to increase *Schlumbergera Truncata* endogenous cytokinins in the early stages of shoot development.

In their native environment, the growths of cacti are limited by the water and nutrient supplies (Castellanos *et al.*, 2018). When plants are grown in pots under commercial technology, it has been hypothesized that water and nutrients are sufficient to compensate for the transpiration rates and nutrient requirements. Regarding nutrients, phosphorus, which would be limited even under fertigation, is characterized by its restricted mobility in soils (White and Hammond, 2008; Shrivastava *et al.*, 2018). To overcome the restricted mobility of soil phosphorus, plants have evolved several features to increase the rhizosphere volume by increasing the absorptive surfaces (Hinsinger *et al.*, 2018). However, most organic substrates used in the ornamental plant industry are almost biologically inert (Di Benedetto and Pagani, 2012). On the other hand, the CAM photosynthetic pathway is energetically costly and requires a higher phosphorus supply (Abrahao *et al.*, 2014), although this photosynthetic pathway is not usual, in succulent-stemmed cactus plants (Hultine *et al.*, 2016). However, these speculations were not validated by our results and are thus a matter for further research.

CONCLUSION

Our present results allow concluding that, from the grower's point of view, the choice to include many initial phylloclades to increase *Schlumbergera truncata* growth in large pots seems a good decision and that a higher number of initial phylloclades than that usually suggested may be included in each pot. However, this may lead to great intraspecific competition, which may, in turn, decrease individual cutting growth. Our results also showed that an early BAP spray application would be a tool to increase cactus biomass accumulation. Finally, our results showed that the RGR of *Schlumbergera truncata* plants grown under commercial management would not be affected by light but rather by the pot root restriction.

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