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Biomass Accumulation in the Fern *Asplenium nidus avis* (L) under Root Restriction

A. Pagani[1], J. Molinari[1], E. Giardina[1] and A. Di Benedetto[1,2*]

[1]*Faculty of Agronomy, University of Buenos Aires, Avenue San Martín 4453 (C1417DSE), Buenos Aires, Argentina.*
[2]*Faculty of Agricultural Sciences, National University of Mar del Plata, Route 226, Km. 73.5 (B7620ZAA), Balcarce, Province of Buenos Aires, Argentina.*

Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

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ABSTRACT

Pot ornamental plant productivity is related to the environmental growth facilities but negatively affected by the pot root restriction syndrome. Most ferns showed a lower relative growth rate and long production cycles (24 months or more) for which growers use small pots to increase yield per unit area of greenhouse. The aim of this work was to analyze growth changes in response to different pot volume in plants of *A. nidus avis* spore-propagated under the hypothesis that it would play a role as an abiotic stress which decrease commercial productivity. Our results showed that the use of big pots increased fresh and dry weight and frond area (the main aesthetic trait). When growth parameters were performed, a higher the frond appearance rate (RLA), the frond area expansion (RLAE) and the frond thickness (SLA) were found in 1500 cm^3 pot as well as the relative growth rate (RGR) and the net assimilation rate. The use of biggest pot for fern cropping stimulated biomass accumulation through a higher capacity to initiate and expand fronds, to increase photosynthetic rates and change photo assimilate partitioning which favor shoots. From the grower´s point of view, our results suggested that higher yields of *A. nidus avis* fern would be reached decreasing root restriction, that is, to use the biggest pot volume from the early transplant from plug trays.

**Corresponding author: Email: dibenede@agro.uba.ar;*

Keywords: Frond initiation; frond expansion; ornamental pteridophytes; photo assimilate partitioning.

1. INTRODUCTION

Asplenium nidus avis fern is native to tropical southeastern Asia and eastern Africa; their main economic value is as popular ornamental foliage plants (nest fern). Pteridophytes are having major advantages as ornamental plant for their propagation and culture due to adaptation to various environmental conditions for a long time. In the floriculture industry of Asian countries such as Sri Lanka, Pteridophytes plays a central role for the future [1]. *A. nidus avis* is a common epiphytic fern, with a short, erect rhizome and a rosette of simple fronds. Fronds roll back as they brown and create a massive leaf nest in the branches and trunks of plants.

For high-input systems such as foliage pot plants, large quantities of water, fertilizers, chemical pesticides, plastics, and labor were used. The main difference in the costs of production are related to the price of the pot [2]. Ornamental plants with a lower relative growth rate and long production cycles (24 months or more), such as ferns [3,4] are cropping at the smaller pot volume and frequently transplanted before to sale. However, plants grown in small pots developed a root restriction intensively described for ornamental potted plants [5] although critical data for ferns is lacking.

A close coordination between root and shoot growth has been previously suggested in ornamental plants [5, 6].The main effect of a root restriction is to decrease both leaf area and photosynthetic rate [7]. As a result, biomass accumulation is limited. In this way, Martin et al. [8] examined numerous physiological parameters in individuals of varying sizes of *A. nidus* and found that the rates of net CO_2 exchange of the fronds measured in situ in the field appeared to increase with plant size.

The need to optimize each growth stage of the *A. nidus avis* sporophyte under commercial environments forces us to understand the effect of abiotic stresses involved. In this way the aim of this work was to analyze growth changes in response to different pot volume in plants of *A. nidus avis* spore-propagated under the hypothesis that it would play a role as an abiotic stress which decrease commercial productivity.

2. MATERIALS AND METHODS

2.1 Plant Material

The experiment was carried out in a greenhouse at the Faculty of Agronomy, University of Buenos Aires, Argentina (34°35'59''S, 58°22'23''W) from September 4th 2016 to May 13th 2017. To reach the proposed objective plantlets of *Asplenium nidus avis* L. from spores grown in 128 plug cell trays^{-1} (11.37 cm^3 cell^{-1}) obtained from a commercial propagator were transplanted to 50, 400, 1000, 1200 and 1500 cm^3 pots filled with a 1:1 (v/v) mix of *Sphagnum maguellanicum* peat and river waste.

2.2 Cultivation and Meteorological Data

Plants were irrigated as needed with high quality tap water (pH: 6.64 and electrical conductivity of 0.486 dS m^{-1}) using intermittent overhead mist and one weekly fertigation (1N:1P:1K:1Ca v/v/v/v) (50 mg L^{-1} N) was included. The fertilization volume per pot varied according to container volume.

Half hourly averages of the air temperature were measured using a HOBO H08-001-02 data logger (Onset Computer Corporation, MA, USA) protected from direct radiation by aluminum foil shades. The mean air temperatures ranged between 22.60°C to 26.07°C. The greenhouse was covered with a black shade-cloth (for 50% full-sunlight) and mean photosynthetic active radiation ranged between 7.10 to 10.60 mol photons m^{-2} day^{-1} during the experiment. The plants were arrangement at a density of 6 plants m^{-2} to avoid mutual shading.

2.3 Sampling and Growth Evaluations

Plants for destructive measurements were harvested at transplant and at 30-day intervals. Roots were washed and roots and frond fresh weights (FW) were recorded. Dry weights (DW) were recorded after drying roots and fronds to constant weight at 80°C for 96 hours. The number of fronds was recorded and each frond area was determined using the ImageJ® (Image Processing and Analysis in Java) software.

The rate of leaf appearance (RLA), the relative growth rate (RGR), the rate of leaf area expansion (RLAE), the mean net assimilation rate (NAR), the mean and leaf area ratio (LAR), the specific leaf area (SLA), the leaf weight rate (LWR), the root/shoot ratio, the leaf area partitioning (LAP) and the allometric coefficients between root and shoot (β) were calculated according to Di Benedetto and Tognetti [9].

2.4 Statistical Analysis

Data (fifty single-pot replication of each treatment) were subjected to a one-way ANOVA for a completely randomized design after checking ANOVA assumptions. Slopes from straight-line regressions of RLAE, RGR, NAR, LAR, LAP and allometric values were tested using the SMATR package.

3. RESULTS

3.1 Fresh Weight Accumulation

At the end of the experiment (240 days about from transplant) the higher fresh weight was found in plants grown in 1500 cm pots with a significant decrease according to pot volume decrease (Fig. 1). Although root fresh weight increased with pot volume, final differences between treatments were related to a higher increase in shoot fresh weight.

3.2 Frond Area

Both individual fronds and total frond areas were lower in 50 cm^3 pot and increased with an increase in pot volume (Table 1) as a result of significant higher RLA and RLAE. SLA on a fresh weight base decreased.

3.3 Dry Weight Accumulation

RGR values were significantly different from plants grown in different pot volumes; data were higher in 1500 cm^3 pot and decreased with pot volume decrease during the experiment. When RGR was separating from their 'physiological' (NAR) and 'morphological' (LAR) components, we found that NAR decreased according pot volume decreased while an inverse pattern for LAR was found. When LAR was separating from SLA (on a dry base) and LWR, we found a decrease in SLA and an inverse pattern in LWR according a pot volume decrease (Table 2).

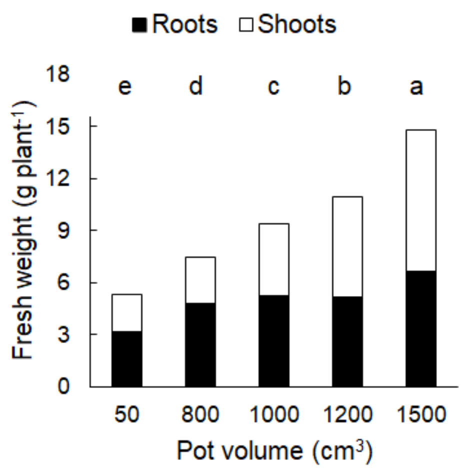


Fig. 1. The effects of five pot volumes on shoot fresh weight at the end of the experiment for the *Asplenium nidus avis* fern.

Different lower case letters indicate significant differences (P < 0.05) between treatments

Table 1. The effects of five pot plug volumes on total and individual leaf area at the end of the experiment, the rate of leaf appearance (RLA), the relative leaf expansion rate (RLAE) and the specific leaf area (SLA) on a fresh weight base

Pot volume (cm^3 pot^{-1})	Frond area (cm^2 $plant^{-1}$)	Frond area (cm^2 $frond^{-1}$)	RLA (fronds $week^{-1}$)	RLAE (cm^2 cm^{-2} day^{-1})	SLA (cm^2 g^{-1})
50	108.25^d	10.33^d	0.0181^c	0.0052^d	52.17^a
800	146.34^c	12.72^c	0.0253^b	0.0070^c	49.27^a
1000	178.96^b	12.23^c	0.0268^b	0.0083^b	43.16^a
1200	184.69^b	14.59^b	0.0283^b	0.0094^b	32.41^b
1500	284.21^a	19.50^a	0.0454^a	0.0113^a	39.81^b

Different lower case letters indicate significant differences (P < 0.05) between treatments

Table 2. The effects of five pot volumes on the relative growth rate (RGR), the net assimilation rate (NAR), the leaf area ratio (LAR), the specific leaf area (SLA) on a dry weight base and the leaf weight ratio (LWR) at the end of the experiment

Pot volume (cm^3 pot^{-1})	RGR ($g\ g^{-1}\ day^{-1}$)	NAR ($g\ cm^{-2}\ day^{-1}$) x 10^{-5}	LAR ($cm^2\ g^{-1}$)	SLA ($cm^2\ g^{-1}$)	LWR ($g\ g^{-1}$)
50	0.0006^c	0.80^c	91.40^a	357.47^a	0.459^e
800	0.0012^c	1.31^c	81.76^b	260.19^b	0.498^d
1000	0.0024^b	3.03^{bc}	79.05^b	239.36^c	0.521^c
1200	0.0035^b	4.43^b	79.30^b	186.38^d	0.597^b
1500	0.0059^a	7.22^a	75.29^b	189.84^d	0.614^a

Different lower case letters indicate significant differences (P < 0.05) between treatments

3.4 Photo Assimilates Partitioning

The high relative partition of photo assimilates to roots during the experiment in response to a limited pot volume determined an increase in root/shoot ratio and higher values in 50 cm^3 pot (Table 3). When LAP and β coefficient increased, photo assimilates were mainly partitioned to roots.

3.5 Growth Parameters Relationships

When plotting the data from all treatments, we found a close direct relationship between RLA (Fig. 2A), RLAE (Fig. 2B), NAR (Fig. 2C), LWR (Fig 2F) and RGR while an inverse relationship between SLA (Fig. 2E), LAP (Fig. 2G), β coefficient (Fig. 2H) and RGR during the experiment. On the other hand, no relationship between LAR and RGR (Fig. 2D) was found.

In the same way, positive relationships between RLA (Fig. 3A), RLAE (Fig. 3B), RGR (Fig. 3C), NAR (Fig. 3D), LWR (Fig. 3G) and root dry weight were found during the experiments. On the other hand, a negative relationship between SLA (Fig. 3F), LAP (Fig. 3H), β coefficient (Fig. 3I) and RDW were found. No relationship between LAR and RDW (Fig. 3D) was found again.

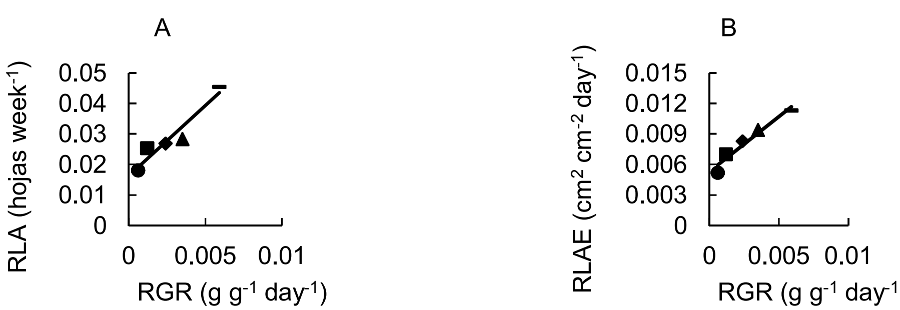
4. DISCUSSION

Although spore germination is very difficult and slow down sporophyte formation [10], we used for our experiment plantlets of *A. nidus avis* L. from spores grown in 128 plug cell $trays^{-1}$ to avoid the hormonal manipulations usually included in micro propagation protocols.

Table 3. Changes in root/shoot ratio, the leaf area partitioning (LAP) and the allometric relationships between roots and shoots for *Asplenium nidus avis* plants grown at five pot volumes during the experiment

Pot volumen (cm^3 pot^{-1})	Root/Shoot ratio	LAP $cm^2\ day^{-1}/g\ day^{-1}$	β
50	1.22^a	652.55^a	1.119^a
800	1.03^a	533.14^b	$1,019^b$
1000	1.02^a	274.26^c	1.045^b
1200	0.68^b	212.31^d	0.935^c
1500	0.64^b	156.59^e	0.730^d

Different lower case letters indicate significant differences (P < 0.05) between treatments



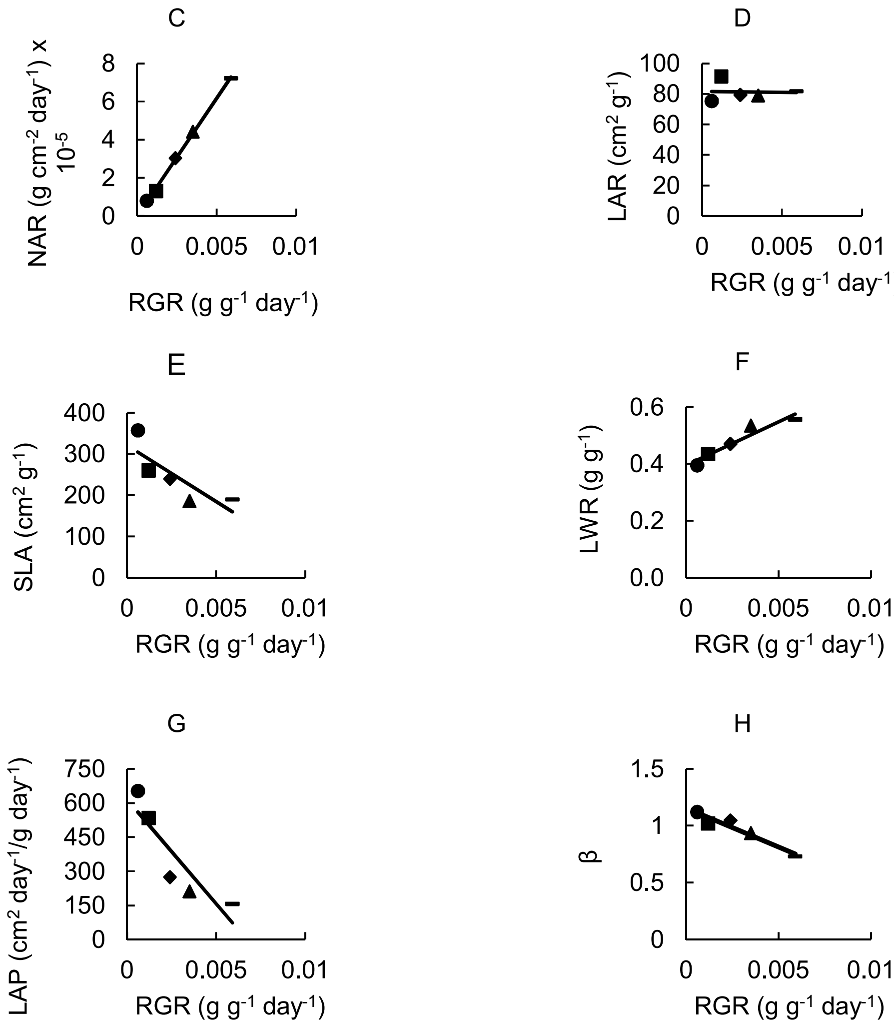
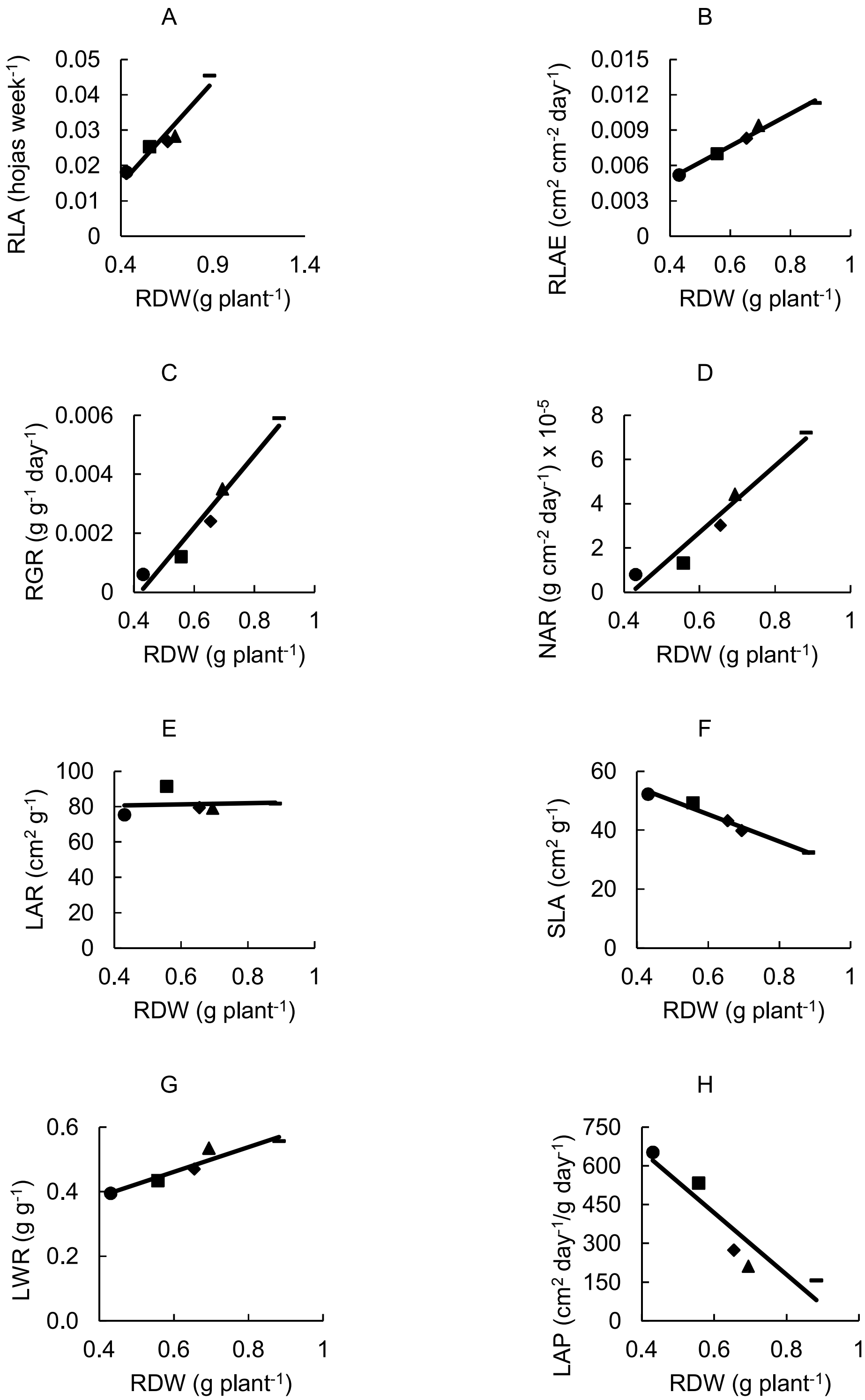


Fig. 2. Relationships between RLA (A), RLAE (B), NAR (C), LAR (D), SLA (E), LWR (F), LAP (G) and the β coefficient (H) and RGR for *Asplenium nidus avis* plants grown at five pot volumes during the experiments

Symbols indicated different pot volumes. •: 50 cm^3; ■: 800 cm^3; ♦: 1000 cm^3; ▲: 1200 cm^3; —: 1500 cm^3. The straight-line regressions were, RLA = 4.60 RGR + 0.016 (r^2 = 0.916; P < 0.001); RLAE = 1.07 RGR + 0.005 (r^2 = 0.947; P < 0.001); NAR = 1233.70 RGR + 0.0003 (r^2 = 0.998; P < 0.001); LAR = 1284.34 RGR + 81.71 (r^2 = 0.002); SLA = -27278.00 RGR + 320.84 (r^2 = 0.677; P < 0.001); LWR = 30.54 RGR + 0.40 (r^2 = 0.902; P < 0.001); LAP = -91.78 RGR + 615.42 (r^2 = 0.799; P < 0.001); β = -68.27 RGR + 1.15 (r^2 = 0.925; P < 0.001)

According to Page [3], the "low-light photosynthetic capacity" and the "slow plant growth rates" are among the main important disadvantages of Pteridophyte biology. Most *Adiantum* species favor shaded and moist conditions and the rates of net CO_2 exchange of the fronds measured in situ in the field appeared to increase with plant size [8]. On the other hand, RGR ranged from 0.22 to 0.35 mg g^{-1} day^{-1} in their native environment and in old plants [4]. Our results in low size plants and under a root restriction related to pot volume showed RGR values, which ranged between 0.6 and 5.9 mg g^{-1} day^{-1} (Table 2). The differences between RGR from high-size plants in their native habitat and low-size plants from a commercial environment (with optimum light, temperature and nutrient supply) in different pot volumes clearly indicate the limited effect of pot restriction on RGR furthermore of plant size. During the monopodial phase, as the leaf size increases from one frond to the next, the apparent phyllochron decreases. The growth rate is always controlled by the source-sink balance within the plant.


A
RLA (hojas week-1)
RDW(g plant-1)
B
RLAE (cm2 cm-2 day-1)
RDW (g plant-1)
C
RGR (g g-1 day-1)
RDW (g plant-1)
D
NAR (g cm-2 day-1) x 10-5
RDW (g plant-1)
E
LAR (cm2 g-1)
RDW (g plant-1)
F
SLA (cm2 g-1)
RDW (g plant-1)
G
LWR (g g-1)
RDW (g plant-1)
H
LAP (cm2 day-1/g day-1)
RDW (g plant-1)

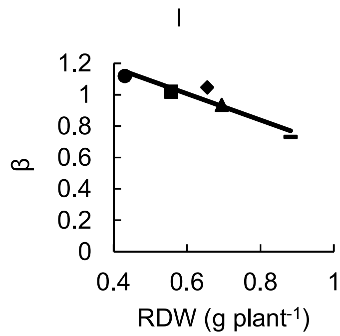


Fig. 3. Relationships between RLA (A), RLAE (B), RGR (C), NAR (D), LAR (E), SLA (F), LWR (G), LAP (H) and the β coefficient (I) and root dry weight (RDW) for *Asplenium nidus avis* plants grown at five pot volumes during the experiments

Symbols indicated different pot volumes. •: 50 cm^3; ■: 800 cm^3; ♦: 1000 cm^3; ▲: 1200 cm^3; ▬ : 1500 cm^3. The straight-line regressions were, RLA = 0.058 RDW - 0.008 (r^2 = 0.922; P < 0.001); RLAE = 0.014 RDW - 0.005 (r^2 = 0.987; P < 0.001); RGR = 0.012 RDW - 0.005 (r^2 = 0.956; P < 0.001); NAR = 15.07 RDW - 6.34 (r^2 = 0.948; P < 0.001); LAR = 3.34 RDW + 79.21 (r^2 = 0.009); SLA = -46.11 RDW + 73.05 (r^2 = 0.974; P < 0.001); LWR = 0.38 RDW + 0.23 (r^2 = 0.900; P < 0.001); LAP = -1134.70 RDW + 11334.80 (r^2 = 0.862; P < 0.001); β = -0.84 RDW + 1.51 (r^2 = 0.886; P < 0.001)

Growers use low pot volume for ferns cropping as a way to optimize yield per unit greenhouse area. However, as was previously indicated for other ornamental plants, root restriction has been defined as a physical stress imposed on the root system when plants are grown in small containers which lead to a pronounced decrease in both root and shoot growth [5]. Results from Fig. 1 are in agreement with previous results in other ornamental vascular plants.

For a foliage potted fern one of the main aesthetic trait is the frond area expanded. Results from Table 1 showed a significant increase for both individual fronds area and total frond area with pot volumes of increasing size in agreement with previous reports in other ornamental foliage plants under a root restriction environment [5]. These results can be explained through a higher RLA and RLAE which are growth parameters that let estimate frond initiation and expansion processes respectively. Fronds are initiated at the peripheral zone of the shoot apical meristem in ferns and the expression of KNOX1 transcription genes [11], is down regulated in the cells of the developing leaf by gibberellin/cytokinin ratio [12].

A. nidus avis plant size is supported by both fresh- and dry-weight accumulation and indicate the time for cropping under unlimited environmental (light, temperature) and technological (water, nutrient) availabilities. Our results suggested a fresh (Fig. 1) and dry weight (data not shown) decrease at the same time pot volume decreased as well. On a dry-weight base these results are supported by changes in RGR and NAR (Table 2). Several attempts have been made to relate net photosynthesis rate to plant productivity in ferns, although it has been pointed out the difficulty of relating leaf photosynthetic rate to yield parameters. As many of the examined species have been grown under field conditions, growth rate determinations based on short term measurements of photosynthesis have proved difficult. Rates of net CO_2 exchange, measured under controlled environmental conditions yet in situ, of attached fronds on individuals of *A. nidus* were very low and were typical of many epiphytic taxa [8]. In this way, NAR (an estimator of plant photosynthesis integral) and RGR (an estimator of photo assimilate accumulation) seems best predictor to fern growth.

On the other hand, the higher pot volume the lower SLA while an inverse result for LWR was found (Table 2). These responses would be interpreted as a mechanism for increasing photosynthetic surface and maximizing photosynthetic capacity, particularly if coupled with a decrease in SLA (higher frond thickness) in agreement with Liao et al. [4]. After entering the leaf, CO_2 faces an intricate pathway to the site of photosynthetic fixation embedded within the chloroplasts. The efficiency of CO_2 flux is hindered by a number of structural and biochemical barriers which, together, define the ease of flow of the gas within the leaf, termed mesophyll conductance, which increased as frond thickness increased as well [13]. If the mesophyll cell space is large enough to avoid excessive cell to cell contact, it is possible to increase mesophyll and chloroplast surface area exposed to intercellular airspace per unit leaf area and improve mesophyll conductance [14]. Previous results on *A. nidus* plants under understory environments did not change SLA as plant size increased [8]. The disagreement with our results can be linked to the root restriction developed during our experiment.

The distribution of biomass among plant organs is not fixed. It is affected by the environment, habit of plant, life span of the plant and, competitive interactions. A limited pot volume decreased root/shoot ratio as a result of a higher photo assimilate partitioning to roots (estimated through a higher LAP and β coefficient from root: shoot allometries) (Table 3) in agreement with previous results in other vascular ornamental plants [5]. The distribution of assimilates within the plant is regulated by source-sink interactions. One of the integrating principles related to allocation is the hypothesis of balanced root and shoot activity. It has been indicated that fast-growing species are more oriented to maximize shoot functioning, whereas the slow growing those as ferns tend to maximize root functioning. This hypothesis would explain why plants of *A. nidus avis* grown under limited pot volume partitioned a higher photo assimilates proportion to roots while those under a less root restriction invest a higher photo assimilate proportion in new leaves.

Data from Fig. 2 suggested that growth parameters such as RLA, RLAE, NAR and LWR showed a strong direct relationship with RGR, but an inverse strong relationship between SLA, LAP and the β coefficient from root: shoot allometries. These last results indicated higher frond thickness and a proportional higher photo assimilate partition to leaves as pot volume increased. The strong correlation between most growth parameters related to frond area expansion and frond anatomical structure and RGR were similar to those found for other ornamental vascular plants [15, 16, 17, 18].

As was indicated in previous reports from our laboratory [5, 18], strong direct relationships between RLA, RLAE, NAR, RGR, LWR and root dry weight were found. On the other hand, a strong inverse relationship between SLA, LAP, β coefficient from root: shoot allometries and root dry weight were found as well (Fig. 3). These results suggested that physiological responses related to limited pot volume would be associated to root system size. The concentration of the cytokinin, endogenous zeatin riboside (mainly synthesized in roots apex), increased in parallel with an increase in root growth rate and reach to a peak in terminal buds just prior to shoot emergence [19], which suggested cytokinin participation as an endogenous signal able to control shoot apical meristem in *A. nidus* [20] in agreement with Di Benedetto et al. [5, 21] in ornamental and vegetables.

5. CONCLUSION

From the grower´s point of view, our results suggested that higher yields of *A. nidus avis* fern would be reached decreasing root restriction, that is, to use the biggest pot volume from the early transplant of plug trays.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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