



Nursery Pre- and Post-Transplant Effects on Tomato (*Solanum lycopersicum* L.) Growth and Yield

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Authors' contributions

This work was carried out in collaboration between all authors.

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ABSTRACT

Tomato yield are related to genotype and commercial crop technology, which gave a significant range of possible results. The aims of this work were to study the effect of cytokinin sprays (BAP) in pre- and post-transplant as a stress-overcoming factor of the pre-transplant cell size for two tomato hybrids. The hypothesis tested were that the use of plug trays for tomato propagation establish a pre-transplant stress which was amplified during the crop cycle, while a pre- and post- transplant BAP spray let to overcoming the root restriction associated to plug cell size. Our results showed that tomato yield would be increased for determined ('Argos') or undetermined ('Superman') tomato hybrids using trays with 50 cells. A 100 mg L⁻¹ BAP foliar spray increase yield in plants from limited plug cell size as well, although the relative effects are related to when a BAP solution was applied (pre- or post-transplant stage) and the plug size used during the nursery cropping. The plug size-BAP relationship change relative yield in tomato through the relative fruit fresh weight in 'Argos' hybrid and both the relative fruit fresh weight and relative fruit number in 'Superman' hybrid. Plants from 50-cell tray¹ showed a higher plant size and a different crop architecture which let to explain, partially at least, the higher fresh-dry weight accumulation rate. The higher relative yield would be positively related to relative growth rate between sowing-transplant and a positive feedback in photo

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assimilates partitioning to plant shoots. Finally, our results showed the mechanisms involved in the plug cell size and BAP relationships, which would be use as a tool for improving fresh tomato yield.

Keywords: Cytokinins; root restriction; biomass accumulation; growth parameters.

1. INTRODUCTION

Tomato is one of the most important vegetable crops worldwide while tomato transplant and stand establishment have received considerable attention from vegetable horticulturists. Although the old Loomis's work [1] indicate that tomato is an easy plant for transplanting, data from the last five decades show that tomato plant size is always greater for plants grown in large containers [2]. Using containers of different sizes often, results in variable degree of root restriction, which determine the detrimental effect of reducing both the morphological and physiological processes in tomato plants. Both tomato shoot, and root growth are positively correlated with container size [3,4]. Although Saito et al. [5] showed that the effects of a root-volume restriction on tomato fruit yield were less than other abiotic stress such as salinity stress, with the development of modern horticulture, root restriction cultivation found in plug culture with limited substrate, has become prevailing in many greenhouses.

There is intense interest in root-to-shoot signalling of environmental stresses, whether root cytokinin biosynthesis or delivery of cytokinins from root to shoot via the xylem [6] can regulate shoot cytokinin concentrations and thence growth and development, especially when the root system is exposed to environmental stress [7]. In this way, Ghanem et al. [8] showed that increasing root-to-shoot cytokinin transport improved vegetative growth and fruit yield of salinized tomato. While the root restriction from plants growing in limited plug cell volume has been associated to an insufficient cytokinin supply, we have previously shown that the exogenous application of the cytokinin 6-benzylaminopurine (BAP) in plants grown in small pots may override the shoot growth limitation due to root restriction [9]. A pre-transplant BAP application increases lettuce, celery and spinach yield [10-12].

The aims of this work were to study the effect of a single BAP sprays on pre- and post-transplant as a root restriction stress overcoming factor and to identify the mechanism involved in the cell size-BAP relationships for two tomato hybrids.

2. MATERIALS AND METHODS

2.1 Plant Material and Experimental Design

Experiments were conducted at a commercial greenhouse placed in Mar del Plata city neighboring, Argentina (37°56' S, 57°46' W) on both tomato (*Solanum lycopersicum* L.) 'Argos' and 'Superman' (F₁ Seminis, Missouri, USA) from November 9th 2014 to February 22th 2015 and repeated once from November 5th 2015 to February 25th 2016. 'Argos' is a determinate or 'bushy' tomato hybrid used for processed food while 'Superman' is an indeterminate or 'vine' tomato hybrid used for production of fresh fruits.

Tomato seeds were germinated and grown in 50, 128 and 288 (55.70, 17.37 and 6.18 cm³ cell⁻¹ respectively) plastic plug trays filled with Klasmann 411® medium (Canadian *Sphagnum* peat moss-perlite-vermiculite 70/20/10 v/v/v). Seedlings were sprayed with BAP (6-benzyl aminopurine) (SIGMA EC 214-927-5) (Sigma-Aldrich Co., St. Louis, MO, USA) solutions (0 and 100 mg L⁻¹) when the first true leaf pair were developed (pre-transplant treatments). Additionally, seedlings without pre-transplant treatment were sprayed with BAP 15 days after transplant (post-transplant treatments). BAP was previously diluted in alcohol 80%. When seedlings reached to the transplant stage, they were transplanted to a typical argiudol soil with 5.2% of organic matter the first 25 cm depth.

Plants were irrigated as needed to compensate 80% relative evaporation-transpiration with high quality tap water (pH: 6.64 and electrical conductivity of 0.486 dS m⁻¹) using intermittent overhead mist. A weekly fertigation (1N:0.5P:1K:0.5Ca v/v) (Stage 2: 50 mg L⁻¹ N; Stage 3-4: 100 mg L⁻¹ N; pot: 150 mg L⁻¹ N) according to Styer and Koranski [13] was included. The volume per pot varied according to container volume.

Weather records (daily maximum-minimum air temperature and global solar radiation) were recorded from a meteorological station 500 meters from the experimental site. The mean air temperatures were 14.04 and 14.24°C

(minimum), 27.63 and 28.52°C (maximum) during the 2014-2015 and 2015-2016 experiments respectively. Mean light were 22.17 and 23.00 MJ m⁻² day⁻¹ during the 2014-2015 and 2015-2016 experiments respectively. The plant density used was five plants m⁻² (1.20 m between rows and 0.25 m between plants).

Plants for destructive measurements were harvested (five per treatment) at the transplant stage, 30 and 60 days after transplant. Roots were washed and root, stem, leaf, petioles and fruits fresh weights (FW) were recorded. Dry weights (DW) were recorded after drying 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 the ImageJ® (Image Processing and Analysis in Java) software.

2.2 Data Analysis

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) was calculated as the slope of the regression of the natural logarithm (ln) of the whole plant on a DW basis versus time (in days) [14]. The rate of leaf area expansion (RLAE) was calculated as the slope of the regression of the ln of total leaf area versus time (in days) [15]. The mean net assimilation rate (NAR), and the leaf area ratio (LAR) [16] 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: k_w : RGR (days⁻¹); W_0 : extrapolated value of total dry weight at time zero (g); A_0 : extrapolated value of leaf area at time zero (cm²); k_a : RLAE (days⁻¹); t : time (in days) at the midpoint of the experimental period and e : base of natural logarithms.

The allometric coefficients between root and shoot were calculated as the slope (β) of the straight-line regression of the ln of the root DW versus the ln of the shoot DW (ln root DW = a + b x ln shoot DW) [17].

Leaf area index (LAI) was calculated using the total leaf area per unit sample soil [18]. The crop growth rate (CGR) relate the total DW with time (in days) and the unit sample soil (m²) [19]. The harvest index (HI) was calculated as the FW of the harvested ears as a percentage of the total shoot FW of the plants [20].

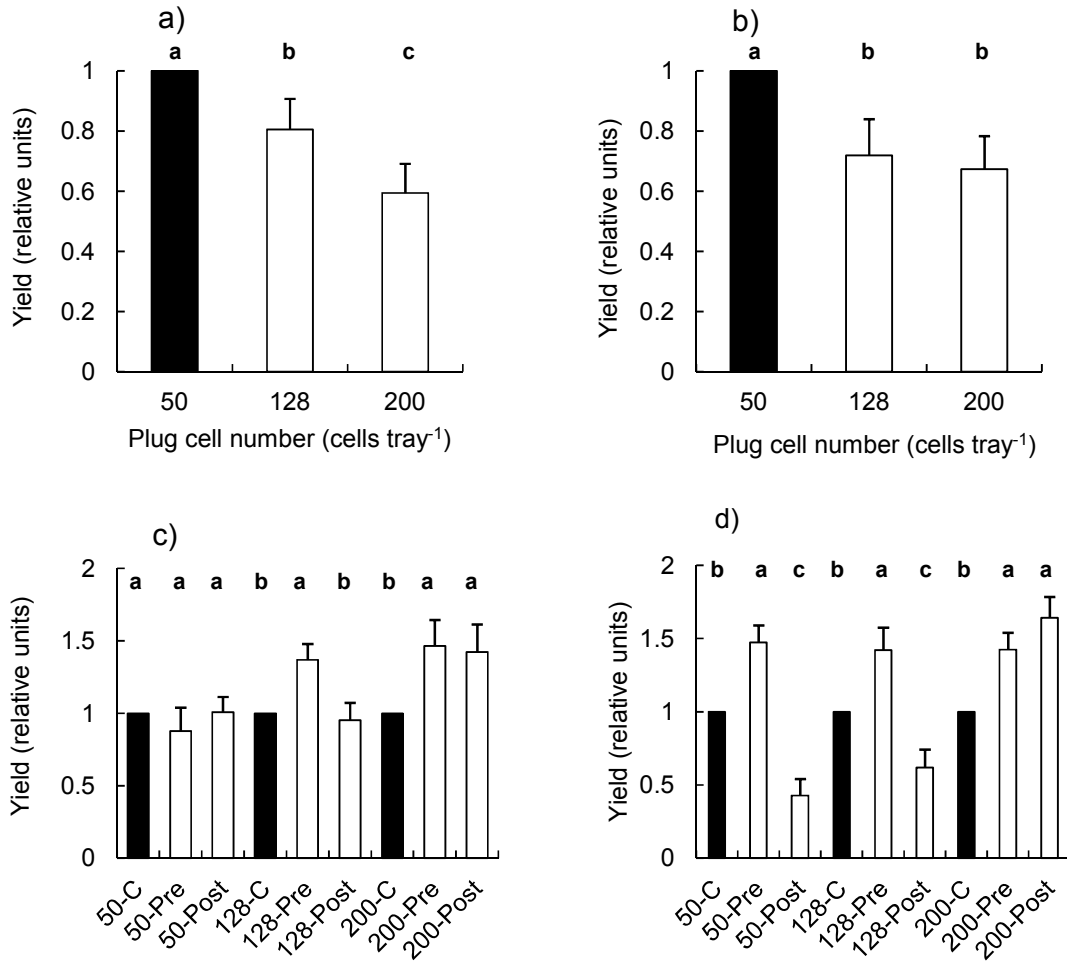
2.3 Statistical Analysis

The experimental design was a randomized factorial with three blocks of four rows of 10 m (1.20 m apart) of each treatment combination (plug cell volume x BAP dose x BAP application time). Since there were no significant differences between the two yearly experiments, they were considered together (n = 6). Data were subjected to three-way analysis of variance (ANOVA). STATISTICA 8 (StatSoft) software was used and the assumptions of ANOVA were checked. Means were separated by Tukey's tests (P ≤ .05). Slopes from straight-line regressions of RLA, RLAE, RGR, NAR, LAR and allometric values were tested using the SMATR package [21].

3. RESULTS

3.1 Yield

When plants from tomato "Argos" genotype were germinated and growth in both 128- and 200-cells plug trays the relative post-transplant yield were 19.5% and 40.6% than those from 50-cell plug trays (Fig. 1a). Although the same qualitative response was found from the "Superman" genotype, the relative yield decrease for 128- and 200-cells plug trays were 28.0% and 33.0% respectively than those from 50-cell plug trays (Fig. 1b). A single pre-transplant or post-transplant BAP spray did not change the relative yield related to 50-cell plug trays controls in "Argos" genotype. However, the same BAP dose (100 mg L⁻¹) at pre-transplant increase relative yield in plants from 128-cells plug trays and both in pre- and post-transplant in plants from 200-cells plug trays (Fig. 1c). In "Superman" genotype, a BAP application increased relative yield when plants from 50-cells plug trays were sprayed at the pre-transplant, but decreased it when plants were sprayed at the post-transplant stage. Plants from 200-cells plug trays showed a relative yield increase when BAP was applied at both pre- and post-transplant (Fig. 1d). Single (Cell size; BAP) and double (Cell size x BAP) effects for yield in the ANOVA showed highly significant differences (P < .001) for both genotypes tested.



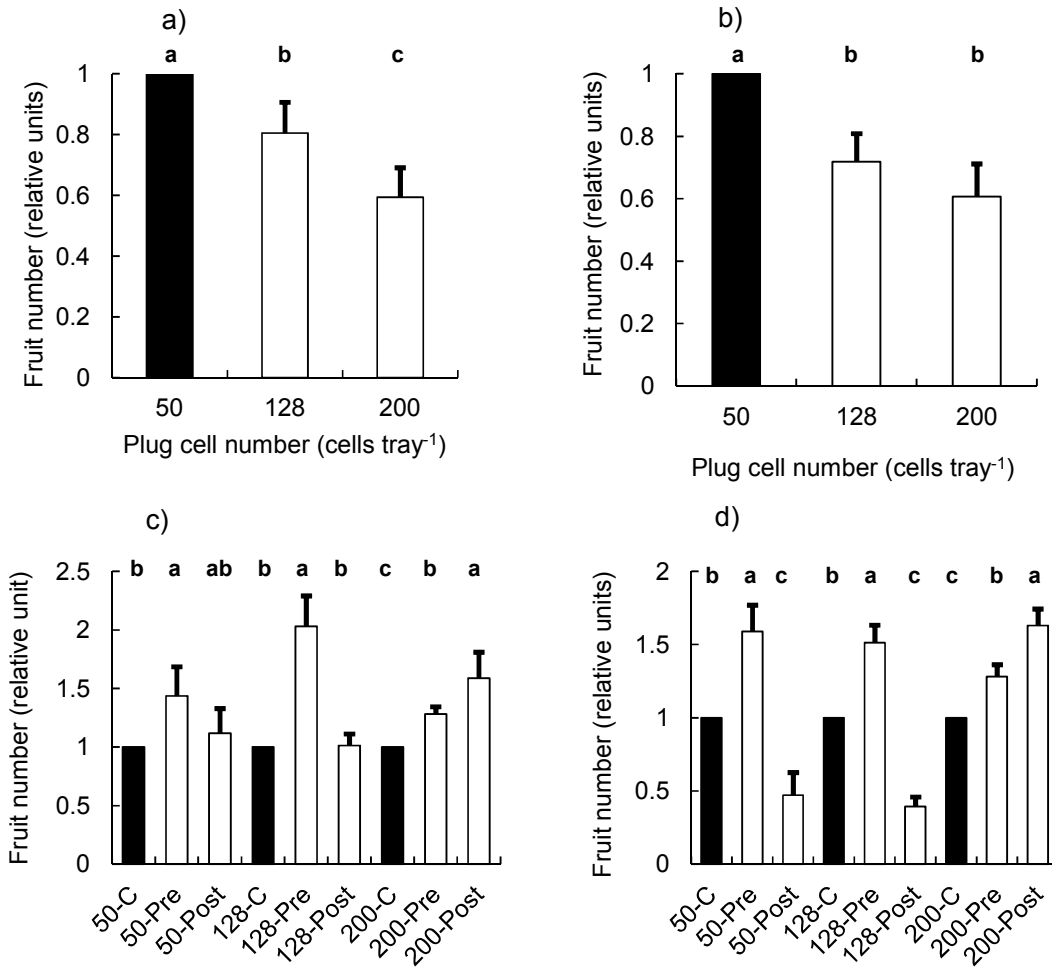
	Significantly	
	ARGOS	SUPERMAN
Cell size	***	***
BAP	***	***
Cell size x BAP	***	***

**Fig. 1. The effect of three plug cell trays (50-, 128- and 200-cells tray⁻¹) and a pre- or post-transplant BAP application (100 mg L⁻¹) on the relative yield of ‘Argos’ (a and c) or ‘Superman’ (b and d) tomato plants. Control plants without treatment: -C. Bars are mean of thirty replications and standard errors were indicated. Lower-case letters indicate statistically significant differences (P < .05). ‘Argos’ tomato yield (kg plant⁻¹) was 4.999 ± 0.791, 4.024 ± 1.010 and 2.971±0.485 for plants from 50-, 128- and 200-cell plug trays. ‘Superman’ tomato yield (kg plant⁻¹) was 5.999±0.536, 4.315 ± 0.717 and 4.039±1.278 for plants from 50-, 128-and 200-cell plug trays
Significance *** .001**

3.2 Fruit Number

The relative fruit number at the end of the experiment showed no significant differences in ‘Argos’ genotype (Fig. 2a) but a 28.0% and

39.0% decrease in plants propagated in 128- and 200-cell plug trays respectively in ‘Superman’ genotype were found (Fig. 2b). A single pre-transplant BAP application increased fruit number in the three-cell size tested both

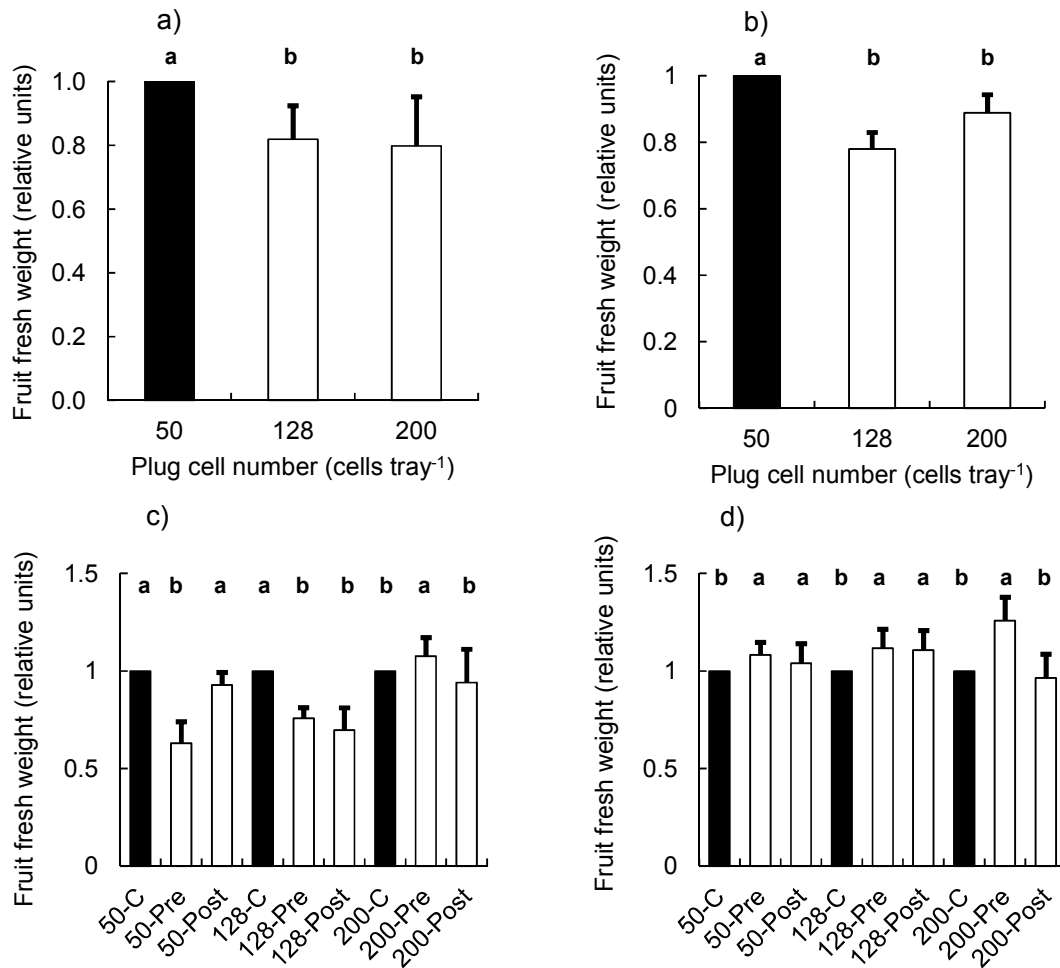


	Significantly	
	ARGOS	SUPERMAN
Cell size	ns	***
BAP	***	***
Cell size x BAP	*	***

Fig. 2. The effect of three plug cell trays (50-, 128- and 200-cells tray⁻¹) and a pre- or post-transplant BAP application (100 mg L⁻¹) on fruit number of ‘Argos’ (a and c) or ‘Superman’ (b and d) tomato plants. Control plants without treatment: -C. Bars are mean of thirty replications and standard errors were indicated. Lower-case letters indicate statistically significant differences (P < .05). ‘Argos’ fruit number plant⁻¹ was 28.57 ± 5.14, 26.27 ± 3.84 and 21.99 ± 2.69 for plants from 50-, 128- and 200-cell plug trays. ‘Superman’ fruit number plant⁻¹ was 37.53 ± 5.97, 32.82 ± 5.10 and 25.05 ± 2.488 for plants from 50-, 128- and 200-cell plug trays
 Significance *** .001 * .05 ‘ns’ No significant

‘Argos’ (Fig. 2c) and ‘Superman’ (Fig. 2d) tomato genotypes. While 50- and 128-cells plug tray fruit number significant decreased with a post-transplant BAP spray in ‘Superman’ genotype, an inverse response in 200-cell plug tray was found. Single (Cell size; BAP) and double (Cell size x BAP) effects for ‘Argos’ genotype in the

ANOVA showed no significant, highly significant differences (P < .001) and significant differences (P < .05) while ‘Superman’ genotype showed highly significant differences (P < .001) for single (Cell size; BAP) and double (Cell size x BAP) effects.



	Significantly	
	ARGOS	SUPERMAN
Cell size	*	*
BAP	*	*
Cell size x BAP	*	*

Fig. 3. The effect of three plug cell trays (50-, 128- and 200-cells tray⁻¹) and a pre- or post-transplant BAP application (100 mg L⁻¹) on fruit fresh weight of ‘Argos’ (a and c) or ‘Superman’ (b and d) tomato plants. Control plants without treatment: -C. Bars are mean of thirty replications and standard errors were indicated. Lower-case letters indicate statistically significant differences (P < .05). ‘Argos’ tomato fruit fresh weight (g plant⁻¹) was 177.38 ± 7.28, 145.28 ± 18.84 and 141.54 ± 27.40 for plants from 50-, 128- and 200-cell plug trays. ‘Superman’ tomato fruit fresh weight (g plant⁻¹) was 169.80 ± 16.96, 132.46 ± 8.55 and 150.94 ± 43.41 for plants from 50-, 128- and 200-cell plug trays
Significance * .05

3.3 Fruit Fresh Weight

“Argos” genotype show an 18.0% and 21.0% fruit fresh weight decrease when plants were grown in 128- and 200-cells plug trays related to those from 50-cell plug trays (Fig. 3a) while fruit

fresh weight decrease was 22.0% and 11% in ‘Superman’ plants (Fig. 3b). Non-significant effects on ‘Argos’ fruit fresh weight with both pre- or post-transplant BAP spray but a significant decrease in 50- and 128-cell plug tray plants were found (Fig. 3c). There is minor changes in

'Superman' fruit fresh weight with a single BAP spray either in the pre- than in the post-transplant stage (Fig. 3d). Single (Cell size; BAP) and double (Cell size x BAP) effects for yield in the ANOVA showed highly significant differences ($P < .05$) for both genotypes tested.

3.4 Leaf Area

The higher total leaf area were found in plants from 50-cell plug tray without differences in plants from 128- and 200-cell plug tray for both tomato genotype tested. A single BAP spray, in the pre-transplant stage, increase leaf area in all 'Argos' and 'Superman' cell size tested, while the same dose in the post-transplant stage decrease leaf area in plants from 50- and 128-cell plug tray for both tomato genotype. Non-significant RLAE differences were found. The higher RLA and LAI were found in plants from 50-cell plug tray. Both RLA and LAI increase when plants from 128- and 200-cell plug tray were sprayed with 100 mg L⁻¹ BAP in pre- and post-transplant. On the other hand, RLA and LAI decrease in plants from 50-cell plug tray with a single BAP spray at any moment (Table 1).

3.5 Biomass Accumulation

The higher RGR was found in plants from 50-cell plug trays at the transplant stage but no significant differences at the end of the experiment. When RGR was disaggregated in NAR and LAR, an inverse relationship were found between them. At the crop level, higher CGR levels in control plants from 50-cell plug trays with a significant increase when they were sprayed with 100 mg L⁻¹ BAP at the pre-transplant stage (Table 2).

3.6 Dry Weight Partitioning

The allometric analysis between roots from Table 3 show higher photo assimilate partitioning to shoots in plants from 50-cell plug tray than those in 128- and 200-cell plug trays. A pre-transplant BAP application increased dry weight partitioning to shoots, as revealed by lower values of the coefficient β while a post-transplant BAP spray give an inverse response. The same pattern response was found in both tomato genotype tested. The harvest index (HI) was higher in control plants from 50- and 128-cells. A positive effect of a pre-transplant BAP was limited to plants from 50-cells plug tray.

4. DISCUSSION

Increasing population and changing dietary habits consumption are placing unprecedented demands on a diet rich in vegetables relate to the human health. In this context, tomato is one of the main crop cultivated in greenhouse worldwide. Tomato yield increase during the last two decades was achieved by extending the cropping period (greenhouse cropping), increasing the fruit load per plant (cultivation practices) and per cropping area [22,23]. However, the presence of different abiotic stress sources during cropping limit future yield increase [24]. The period and development of stress, stages of the plant, and abiotic factors may influence the stress response [25]. Our results showed that the root restriction related to volume cell plug size is a technological stress source and decrease yield 19.5-40.6% or 28.1-32.7% for the tomato determinate hybrid 'Argos' or the indeterminate hybrid 'Superman' respectively (Figs. 1a, b) in plants grown in 128- and 200-cell tray⁻¹ compared with plants from 50-cell tray⁻¹.

Matsuo et al. [26] showed that cytokinins play important roles in tomato fruit development, especially cell division. In previous reports, we have suggested that an exogenous BAP spray can override the abiotic stress related to the plug cell volume in vegetables [11,12,27] and ornamental plants [9,28,29]. Data from Fig. 1 (c and d) showed that a pre-transplant BAP spray increase yield in near 42% in plants from limited plug cell tray (128- and 200-plug cell tray⁻¹) but the same BAP treatment give not significant increase in plants from non-limiting plug cell size (50-cells tray⁻¹) for the determined tomato hybrid 'Argos'. A post-transplant BAP spray in 'Argos' give no yield changes (50-or 128-cell tray⁻¹ plants). In the indeterminate 'Superman' hybrid, a pre-transplant BAP ever increased yield in plants from 50-, 128- or 200- cell tray⁻¹ (47.4, 42.0 and 42.5% respectively) with a yield decrease of 57.1 and 38.11% in plants from 50- and 128-cell tray⁻¹ when a post-transplant BAP spray were used. These results are in agreement with a previous report in celery and lettuce [10].

Tomato yield is positively related to fruit number, fruit size and fruit fresh weight. A root restriction stress did not change 'Argos' and 'Superman' fruit size (data not shown) but significantly decrease fruit number (Fig. 2) and fruit fresh weight (Fig. 3) in plants from 128- and 200-cell tray⁻¹ compared to those plants from

Table 1. Total leaf area at the end of the experiment and changes in RLAE, RLA and LAI in two tomato genotypes grown at three plug cell trays (50-, 128- and 200-cells tray⁻¹) and sprayed or not (control plants) with 100 mg L⁻¹ BAP solutions at pre- or post-transplant stage. Different lower case letters indicate significant differences (P < .05) between control and BAP-sprayed plants, while different capital letters indicate significant differences (P < .05) between different BAP treatments for each plug cell number. The probability of the slope being zero for RLAE and RLA was P < .001

	Leaf area cm ² plant ⁻¹		RLAE cm ² cm ⁻² day ⁻¹		RLA leaves week ⁻¹		LAI m ² m ⁻²	
	ARGOS	SUPERMAN	ARGOS	SUPERMAN	ARGOS	SUPERMAN	ARGOS	SUPERMAN
50 plug cells tray ⁻¹								
Control	2,800.40 ^{aA}	2,034.23 ^{bA}	0.106 ^{aA}	0.102 ^{aA}	1.875 ^{aB}	1.850 ^{aA}	1.400 ^{bA}	1.017 ^{bA}
Pre-transplant	3,589.43 ^{bC}	2,473.98 ^{aA}	0.110 ^{aB}	0.105 ^{aA}	1.475 ^{aC}	1.575 ^{bA}	1.795 ^{aA}	1.237 ^{aA}
Post-transplant	1,690.91 ^{bB}	1,247.38 ^{cB}	0.099 ^{bA}	0.093 ^{bA}	1.400 ^{aB}	1.500 ^{bB}	0.845 ^{cB}	0.624 ^{cC}
128 plug cells tray ⁻¹								
Control	1,729.39 ^{bC}	1,495.23 ^{bB}	0.097 ^{bB}	0.097 ^{aA}	1.500 ^{bA}	1.325 ^{bB}	1.093 ^{bB}	0.765 ^{cB}
Pre-transplant	3,404.13 ^{aA}	1,883.45 ^{aB}	0.108 ^{aA}	0.101 ^{aA}	1.850 ^{aA}	1.525 ^{aA}	1.317 ^{aB}	1.166 ^{aB}
Post-transplant	1,184.55 ^{cC}	985.92 ^{cC}	0.093 ^{bA}	0.089 ^{aA}	1.775 ^{bA}	1.400 ^{bC}	1.057 ^{bA}	0.912 ^{bA}
200 plug cells tray ⁻¹								
Control	1,861.73 ^{bB}	1,530.47 ^{cB}	0.091 ^{aB}	0.096 ^{aA}	1.450 ^{bB}	1.425 ^{bB}	0.665 ^{bC}	0.748 ^{bB}
Pre-transplant	2,633.96 ^{aB}	2,332.55 ^{aA}	0.105 ^{aA}	0.103 ^{aA}	1.725 ^{aB}	1.625 ^{aA}	0.792 ^{aC}	0.942 ^{aC}
Post-transplant	2,114.85 ^{bA}	1,823.63 ^{bA}	0.101 ^{aA}	0.100 ^{aA}	1.700 ^{aA}	1.675 ^{aA}	0.602 ^{bC}	0.693 ^{bB}

Table 2. The Relative Growth Rate (RGR), the Net Assimilation Rate (NAR), the Leaf Area Ratio (LAR) and Crop Growth Rate (CGR) in two tomato genotypes grown at three plug cell trays (50-, 128- and 200-cells tray⁻¹) and sprayed or not (control plants) with 100 mg L⁻¹ BAP solutions at pre- or post-transplant stage. Different lower case letters indicate significant differences (P < .05) between control and BAP-sprayed plants, while different capital letters indicate significant differences (P < .05) between different BAP treatments for each plug cell number. The probability of the slope being zero for RGR, NAR, LAR and CGR was P < .001

	RGR (sowing-transplant) g g ⁻¹ day ⁻¹		RGR (transplant-harvest) g g ⁻¹ day ⁻¹		NAR g cm ⁻² day ⁻¹ x 10 ⁻⁴		LAR cm ² g ⁻¹		CGR g m ⁻² day ⁻¹	
	ARGOS	SUPERMAN	ARGOS	SUPERMAN	ARGOS	SUPERMAN	ARGOS	SUPERMAN	ARGOS	SUPERMAN
50 plug cells tray ⁻¹										
Control	0.450 ^{aA}	0.399 ^{aA}	0.036 ^{aB}	0.055 ^{aB}	17.70 ^{bB}	30.48 ^{bA}	20.34 ^{aB}	21.39 ^{aA}	24.78 ^{bA}	310.02 ^{bA}
Pre-transplant	0.419 ^{aA}	0.366 ^{aA}	0.047 ^{aB}	0.065 ^{aA}	44.96 ^{aA}	38.16 ^{aB}	10.41 ^{bC}	14.52 ^{bA}	80.69 ^{aA}	472.04 ^{aB}
Post-transplant			0.035 ^{aB}	0.048 ^{aB}	13.42 ^{bB}	35.73 ^{aA}	25.90 ^{aB}	13.46 ^{bB}	11.35 ^{cB}	222.84 ^{cB}
128 plug cells tray ⁻¹										
Control	0.348 ^{aB}	0.358 ^{aA}	0.059 ^{aA}	0.068 ^{aA}	19.14 ^{bB}	33.61 ^{bA}	29.63 ^{aA}	19.18 ^{aA}	20.93 ^{bA}	257.20 ^{cB}
Pre-transplant	0.367 ^{aA}	0.339 ^{aA}	0.057 ^{aA}	0.069 ^{aA}	38.77 ^{aB}	49.68 ^{aA}	15.29 ^{bB}	13.78 ^{bA}	51.06 ^{aB}	579.41 ^{aA}
Post-transplant			0.067 ^{aA}	0.064 ^{aA}	23.89 ^{bA}	38.45 ^{bA}	28.16 ^{aB}	17.84 ^{aB}	25.26 ^{bA}	350.59 ^{bA}
200 plug cells tray ⁻¹										
Control	0.347 ^{aB}	0.334 ^{aB}	0.059 ^{aA}	0.059 ^{aB}	22.33 ^{bA}	24.72 ^{bB}	26.36 ^{bA}	25.20 ^{aA}	19.31 ^{aA}	184.81 ^{bC}
Pre-transplant	0.369 ^{aA}	0.350 ^{aA}	0.059 ^{aA}	0.062 ^{aA}	31.12 ^{aB}	34.16 ^{aB}	19.07 ^{cA}	17.36 ^{bA}	21.85 ^{aC}	321.69 ^{aC}
Post-transplant			0.059 ^{aA}	0.054 ^{aB}	20.70 ^{bA}	21.68 ^{bB}	37.55 ^{aA}	31.68 ^{aA}	21.26 ^{aA}	106.87 ^{cC}

Table 3. Allometric relationships between roots versus shoots and Harvest Index (HI) in two tomato genotypes grown at three plug cell trays (50-, 128- and 200-cells tray⁻¹) and sprayed or not (control plants) with 100 mg L⁻¹ BAP solutions at pre- or post-transplant stage. The allometric slope straight-line (β) are indicated. Different lower case letters indicate significant differences ($P < .05$) between control and BAP-sprayed plants, while different capital letters indicate significant differences ($P < .05$) between different BAP treatments for each plug cell number. The probability of the slope being zero was $P < .001$.

	β		HI	
	ARGOS	SUPERMAN	ARGOS	SUPERMAN
50 plug cells tray ⁻¹				
Control	0.424 ^{bB}	0.456 ^{bB}	0.614 ^{bA}	0.604 ^{bA}
Pre-transplant	0.276 ^{cB}	0.387 ^{cB}	0.691 ^{aA}	0.655 ^{aA}
Post-transplant	0.732 ^{aA}	0.522 ^{aB}	0.588 ^{cA}	0.597 ^{aA}
128 plug cells tray ⁻¹				
Control	0.738 ^{bA}	0.514 ^{bA}	0.570 ^{aA}	0.614 ^{aA}
Pre-transplant	0.563 ^{cA}	0.417 ^{cA}	0.594 ^{aB}	0.588 ^{aB}
Post-transplant	0.798 ^{aA}	0.603 ^{aA}	0.549 ^{bB}	0.528 ^{bA}
200 plug cells tray ⁻¹				
Control	0.731 ^{aA}	0.598 ^{aA}	0.504 ^{aB}	0.519 ^{bB}
Pre-transplant	0.502 ^{bA}	0.425 ^{bA}	0.532 ^{aB}	0.633 ^{aA}
Post-transplant	0.698 ^{aB}	0.551 ^{aB}	0.506 ^{aC}	0.612 ^{aA}

50-cell tray⁻¹. These results showed that plants which to endure a pre-transplant abiotic stress such as a root restriction, falls to get over it. The effect of a single BAP spray had a higher effect on fruit number than fruit fresh weight which can be explained by the common control of cytokinins on apical dominance [30].

Ismail & Dalia [31] showed that tomato fruit fresh weight was reduced when plants were grown with decreasing post-transplant root zone volumes, which was associated with a reduction in water potential and photosynthetic rate. Linear relationships between relative yield and relative transpiration were found in tomato [32] while Machado and Oliveira [33] showed that commercial yield was higher for the treatment where the quantity of water applied was the greatest. However, Schachtman & Goodger [34] have indicated that as soils become dry, root-sourced signals are transported via the xylem to leaves and result in reduced water loss and decreased leaf growth as well. In this way, Alvarez et al. [35] found a decrease in zeatin and zeatin riboside concentrations in xylem sap coming from roots of drought stressed plants as compared to well-watered controls. Cytokinins are thought to be synthesized mainly in the root tips, and translocated to the shoot meristematic cells via xylem vessels [36] for which cytokinins have also been thought to act as a long distance signal [37, 38]. Decreased cytokinin export from roots in drying soil might provide a root-to-shoot signal affecting shoot physiology [7]. On the

other hand, plants grown in small cells and pots show a well developed root system with root girdling growth around the cell [39] which decrease root ramification and cytokinin synthesis points. Root restriction often depresses photosynthetic capacity. It is likely that root restriction induced depression of photosynthesis was mimicked by water stress [40]. Alsadon [3] showed that using containers of different sizes often results in variable degree of root restriction, which can cause negative responses on plant height, leaf area and dry weight.

Canopy development and crop production are interrelated. Leaf growth is an important process in crop production systems, characterized by the production rate of new leaves, the rate of leaf expansion and the final size of each one. In this way, Table 1 shows the higher cell size the higher RLA and RLAE. On the other hand, a single pre-transplant 100 mg L⁻¹ BAP spray increase both growth parameters in limited plug cell tray (200-cell tray⁻¹). As a result, plants from 50-cell tray⁻¹ give the higher total leaf area per plant and canopy LAI (Table 1). The number of leaves preceding the first inflorescence in tomato change according environmental factors such as temperature [4,41] but our results indicate that the endogenous hormonal balance related to the pre-transplant root restriction and exogenous increase in apical cytokinin are involved. Partitioning to the vegetative parts determining LAI and hence future light interception and dry matter production.

Interactions (feedback mechanisms) between dry matter production and dry matter distribution in tomato can be distinguished. The longer leaf area per plant the greater the amount of carbon fixed and transported. Shi et al. [40] indicated that root restriction depresses photosynthetic capacity in agreement with our NAR data. Gross photosynthetic capacity of greenhouse-grown tomato plants often decreased as the leaf aged [42] for which a greater RLA would maintain high photo assimilate acquisition. Table 2 show that both RGR and NAR increased under non-limited cytokinin supply and let to explain the higher crop CGR. The cytokinin function has been linked to different abiotic stresses [43,44]. Genetic engineering approaches were used to confirm the role of cytokinins in plant morphogenesis, and results revealed that cytokinin organ imbalance results into morphological abnormalities and a crucial effect on shoot/root ratio [45].

Most of the tomato dry matter of the fruit therefore comes from assimilates photosynthesized in the leaves. The mechanisms, which control the intake of carbon and water in the fruit, therefore play an essential role in determining the dry matter concentration of the fruit and therefore its final quality [46]. Biomass partitioning among organs depends on their sink strengths, i.e. their capacity to attract assimilates. The sink strength increases proportionally to its size at the early growth stage and decreases by dampening when it approaches the final size [47]. Generally, two approaches has been used: growth rate analysis of harvested organs and analysis of harvest index (HI) increase over time [20]. Root-shoot allometries and HI at the harvest stage from table 3 indicate that both descriptors of harvest-organ in tomato decreased under limiting cytokinin supply.

Our data show that tomato plant productivity is enhanced by sink strength and source activity, which are regulated by a complex signaling network encompassing both environmental and technological factors (pre-transplant root restriction) but mediated by endogenous signals such as cytokinins. These signaling pathways determine the direction of photo assimilate flow (Table 3) and metabolic pathways (Table 2). Growth analysis and source–sink interactions modulate carbon assimilation and partitioning during growth and development, which determines the pattern of carbohydrate allocation

throughout the plant and has a pivotal role in determining tomato crop productivity (Fig. 1). Plant productivity can be enhanced by source activity (high photosynthesis or nutrient remobilization rates) and sink strength (highly competitive capacity for import of photo assimilates). Consequently, a carbon imbalance caused by insufficient sink strength or slow sugar export leading to the accumulation of carbohydrates in source organs will result in feedback downregulation of photosynthetic efficiency in leaves [48]. Sink strength and source activity can be altered by endogenous hormones and environmental factors [49]. To elucidate these mechanisms is a prerequisite for devising hormonal crop management or genetic manipulation strategies of source–sink nutrient allocation toward crop improvement. On the other hand, the phytohormone engineering has the potential for producing high-yielding and abiotic stress-tolerant crops, which provides new opportunities to maintain sustainable crop production to feed the whole world under changing environmental conditions [44].

5. CONCLUSIONS

The root restriction associated with plug-cell volume has been previously documented in vegetables and ornamentals, but recently has been considered as a technological stress source. From a grower's point of view, limiting root restriction is essential for crop productivity. Because our results in two tomato genotypes with different growth habit showed that, the abiotic stress imposed by the plug-cell volume constitutes an interactive process associated with the cytokinins synthesis. One expensive option is to increase the pre-transplant plug-cell volume. In contrast, a single pre-transplant 100 mg L⁻¹ BAP spray can partially override plug cell root restriction.

The cytokinin engineering has the potential for producing high-yielding and abiotic stress-tolerant crops, which provides new opportunities to maintain sustainable crop production to feed the whole world under changing dietary habits consumption. Plant responses to cytokinins have been evaluated most often via their external application; stressful conditions are also known to enhance their endogenous levels via uptake and enhanced biosynthesis. Although phytohormone engineering is promising for plant biologists, there is still a long way to go before the technology can reach its full potential.

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COMPETING INTERESTS

Authors have declared that no competing interests exist.

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