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Physiological Mechanism Involved in the Response to Four Lettuce Varieties to a Pre-transplant Root Restriction and a 6, benzyl aminopurine (BAP) Spray

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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

Vegetable yield is positively related to the environment and negatively affected by the pot root restriction during both the nursery and post-transplant stages. Root restriction is a physical stress imposed on the root system when plants are grown in small containers, which leads to a pronounced decrease in root and shoot growth at both the transplant and pot stages. Based on the assumption that the plant responses are mainly associated with a negative hormonal signaling from roots, some researchers have proposed that these abiotic stresses may be overridden by using a pre-transplant spray with benzyl amino purine (BAP), a synthetic cytokinin able to regulate plant metabolism. Although the physiological mechanisms induced by BAP have been described, the implementation of commercial applications of BAP for vegetables is still a pending issue. The aim of this work was to analyze growth changes in four lettuce genotypes in the presence of

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different root restrictions degree by the use of different plug cell volumes but sprayed with a single BAP spray under the hypothesis that it would play a role as abiotic stress alleviators. Our results showed that the higher biomass accumulation in lettuce plants non root-limited and BAP-sprayed ones are supported by higher photosynthetic rates, by higher leaf number initiation and expansion and by photo assimilate partition to shoots. Understanding the plant responses to this hormonal manipulation and the physiological mechanism involved will allow adjusting the agronomic advice for different vegetables and reaching commercial yields to each of them.

Keywords: Cytokinin; growth parameters; nursery; transplant.

1. INTRODUCTION

In most vegetables, transplanting has replaced direct seeding. The issue of container size is extremely important to both transplant producers and transplant consumers. A trend among many commercial transplant producers is toward more cells per tray (smaller containers), which increases the number of plants produced, while reducing the need to develop more transplant production space. This trend also reduces propagation costs per plant, since production costs are directly related to container size and type. While the use of smaller containers may improve the efficiency of transplant production, it is clear that plants grow in smaller root volumes will develop a root restriction syndrome which remains under post-transplant to field conditions. In general, as container size increases plant leaf areas, shoot biomass and root biomass increase [1].

Roots have a high capacity to sense the physicochemical parameters of the soil and to adjust their development and performance accordingly, thereby playing an essential role in maintaining the nutritional and development functions of the plant under abiotic stresses. On the other hand, an important mediator of shoot biomass production can be the supply of signal molecules from the root system. Although the effective cytokinin concentration is the result of endogenous and environmental signals [2], cytokinins are mainly synthesized in the roots [3] and move through the stem xylem to the shoot apical meristem, where they exert a major regulatory influence on growth. A decrease in cytokinin supply from the root to the shoot may inhibit leaf growth and that a low cytokinin content would promote root growth and thus the root-shoot ratio [4].

Lettuce (*Lactuca sativa* L.) is the most commonly consumed fresh leafy vegetable and one of the main crops grown under greenhouses [5,6]. A 200 to 288 plug cell tray has been usually used for lettuce. Studies by Coro et al. [7] in the large summer butter head lettuce 'Dolly' showed an increase in yield (expressed as aerial fresh weight 60 days from transplanting) in plants sprayed with the synthetic cytokinin 6, benzyl aminopurine (BAP) at the pre-transplant stage (with a maximum increase at the 100 mg L^{-1} dose), but a decrease in those sprayed at the post-transplant stage. The final significant differences in lettuce yield found may be explained by the significant relationships between the time of application of BAP and the plug cell volume.

The need to optimize efficiency in collecting scientific data limits the number of genotypes involved in each experiment. However, the high lettuce genotypes number available force to ask to what extent the responses found in a specific genotype are able to duplicate in the rest of the available ones. To answer it, the aim of this work was to analyze growth changes in four lettuce genotypes in the presence of different root restrictions degree by the use of different plug cell volumes but sprayed with a single BAP spray under the hypothesis that it would play a role as abiotic stress alleviators.

2. MATERIALS AND METHODS

2.1 Plant Material

The experiments were carried out in a greenhouse at the Faculty of Agronomy, University of Buenos Aires, Argentina (34°28'S) from August 2th to November 3th 2017 and repeated once from August 5th to November 3th 2018.

To reach the proposed objectives two butter head lettuce (*Lactuca sativa* L.) seeds, such as, 'Lores' (Vilmorin, France) and 'Sandrine' (Clause-Tézier, France), and two crisp head lettuce seeds, such as 'Taina' (Sakata, Japan)

and 'Luana' (Sakata, Japan) were used. Seeds were germinated and grown in 50, 128 and 288 (55.70, 17.37 and 6.18 cm^3 $cell^{-1}$ 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-benzylaminopurine) (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 7 days after transplant (post-transplant treatments). BAP was previously diluted in alcohol 80%.

2.2 Cultivation and Meteorological Data

When seedlings reached to the transplant stage, they were transplanted into 3 litres pots filled with a 1:1 (v/v) mix of *Sphagnum maguellanicum* peat and river waste during near 60 days (post-transplant stage).

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: 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) was included. The 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 16.09°C to 25.05 and mean photosynthetic active radiation ranged between 15.22 to 27.33 mol photons m^{-2} day^{-1} during the experiments. The plants arrangement at a density of 6 plants m^{-2} avoided mutual shading.

2.3 Sampling and Growth Evaluations

Plants for destructive measurements were harvested (ten per treatment) at emergence and at 7-day intervals during the pre-transplant stage. After transplant, they were harvested at 20-days intervals. Roots were washed and root, stem, leaf and petioles 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.

The rate of leaf appearance (RLA), the relative growth rate (RGR), the rate of leaf area expansion (RLAE), the mean net assimilation rate (NAR) and the mean and leaf area ratio (LAR) were calculated according to Di Benedetto and Tognetti [8].

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 *vs*. the ln of the shoot DW (ln root DW = a + b x ln shoot DW).

Glucose content analysis was performed at the final sampling of the pot experiments (leaves) using the phenol-sulphuric method. The concentrated sulfuric acid breaks polysaccharides, which react with phenol to produce a yellow-gold colour. A standard carbohydrate curve is performed and the absorption was measured with a Carl Zeiss DMR spectrophotometer at 490 nm.

2.4 Statistical Analysis

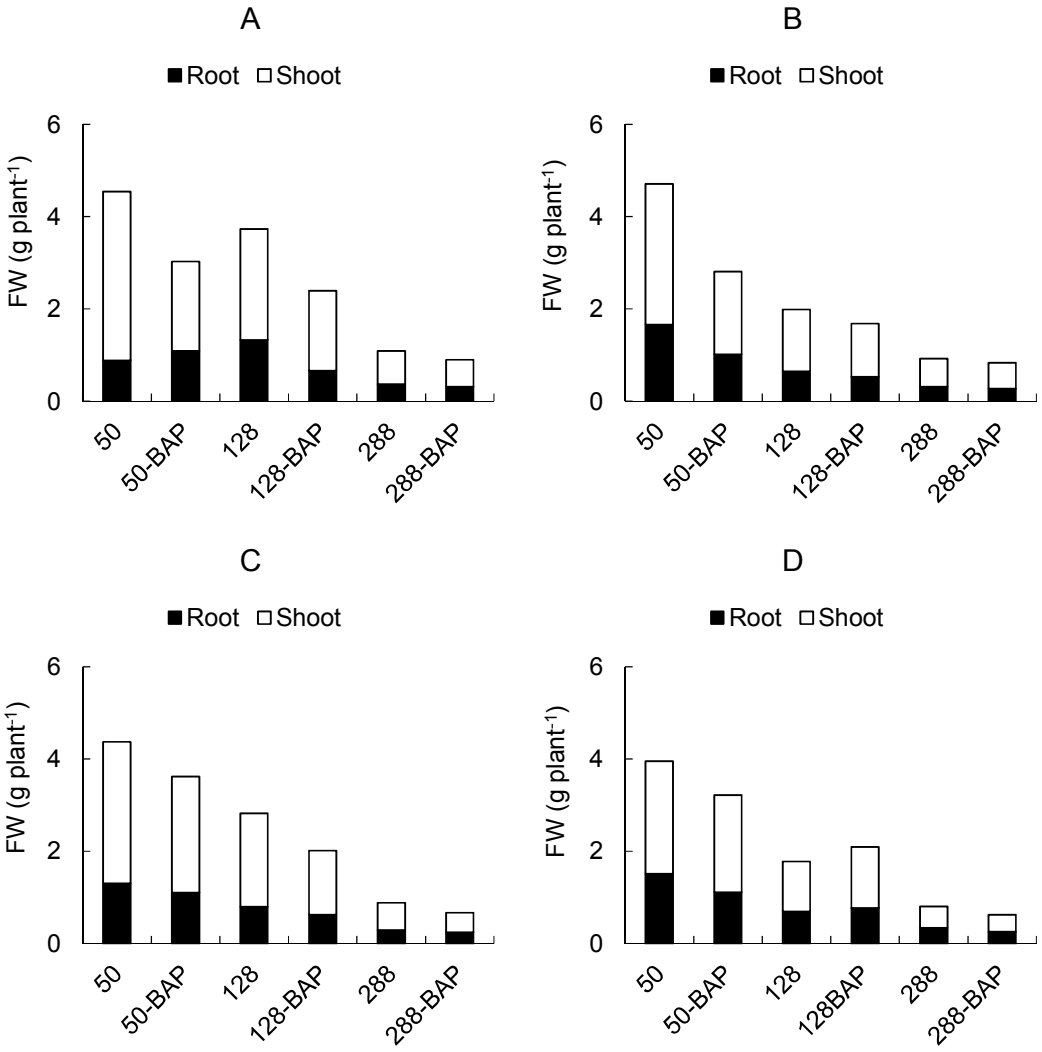
The experimental design was a randomized factorial with three blocks of five single-pot replication of each treatment combination (plug cell volume × BAP application × lettuce genotype). Since there were no significant differences between the two yearly experiments, they were considered together (n = 180). Data were subjected to three-way analysis of variance (ANOVA). STATISTICA 8 (StatSoft) software was used and the assumptions of ANOVA were checked. Least significant differences (LSD) values were calculated. Means were separated by Tukey's tests ($P \leq 0.05$). Slopes from straight-line regressions of RLAE, RGR and allometric values were tested using the SMATR package [9].

3. RESULTS

3.1 Fresh Weight Accumulation

Both at the transplant stage (Fig. 1) and the end of the experiments (60 days from transplant) (Fig. 2) lettuce plants from the lower plug cell volume (288-cells trays) significantly decreased both shoot and root FW in all lettuce genotype tested. Plants BAP-sprayed decreased FW especially in those from 50- and 128-plug cell tray at the transplant stage (Fig. 1). However, at

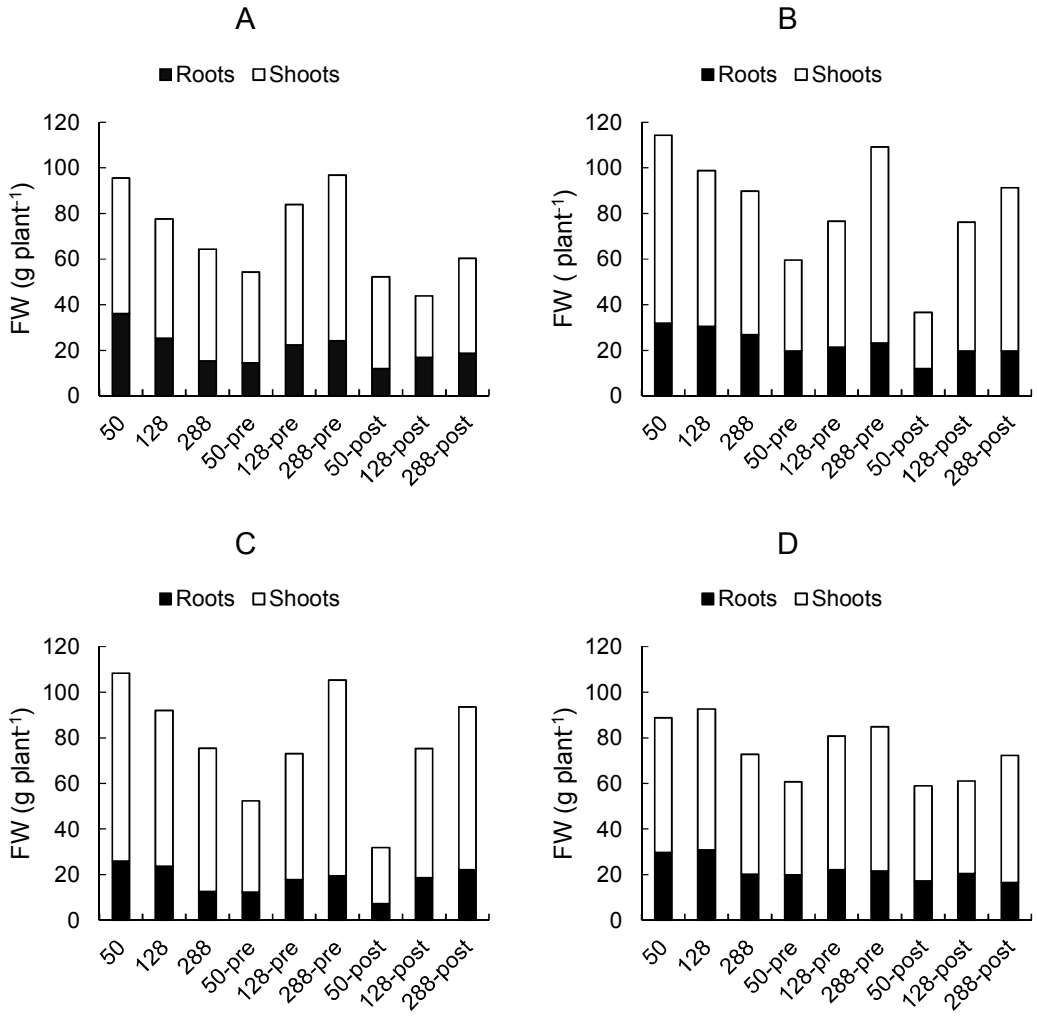
the end of the pot experiments, plants from 50-cells decreased FW but those from 128- and 288-cells increased FW (Fig. 2). Post-transplant BAP-sprayed plants showed a smaller response. Fig. 3 showed biomass accumulation related to the plug cell volume at the transplant stage and the new root restriction related to pot cell volume during the post-transplant experiments.



ANOVA	Roots	Shoots
Cell volume (CV)	***	***
BAP	***	***
Genotype (G)	**	**
CV x BAP	**	**
CV x G	**	**
CV x BAP x G	ns	ns

*Significance: *** p ≤ 0,001; ** p ≤ 0,01; 'ns' No significant*

Fig. 1. The effects of three plug cell volumes (50-, 128- and 288-cells tray^{-1}) and a pre-transplant BAP spray (100 mg L^{-1}) on shoot fresh weight at the transplant stage (nursery experiment) for four lettuce genotypes. The significance of interactions (ANOVA) has been indicated. A: Lores; B: Sandrine; C: Taina and D: Luana



ANOVA	Roots	Shoots
Cell volume (CV)	***	***
BAP	***	***
BAP time (BAP_t)	***	***
Genotype (G)	***	**
CV x BAP	**	**
CV x BAP_t	**	**
CV x G	**	**
CV x BAP x G	ns	ns

*Significance: *** p ≤ 0,001; ** p ≤ 0,01; 'ns' No significant*

Fig. 2. The effects of three plug cell volumes (50-, 128- and 288-cells tray^{-1}) and a pre- or post-transplant BAP spray (100 mg L^{-1}) on shoot fresh weight at the end of the pot experiment (60 days from transplant) for four lettuce genotypes. The significance of interactions (ANOVA) has been indicated

When the mean shoot FW was plotted against the mean root FW for all treatments (controls and BAP-sprayed plants), positive correlations were found for all lettuce genotypes tested both at the transplant stage (Fig. 4A) and at the end of the pot experiments (Fig. 4B).

Fig. 3. Lettuce plants at the transplant stage and in three different times during the pot experiments

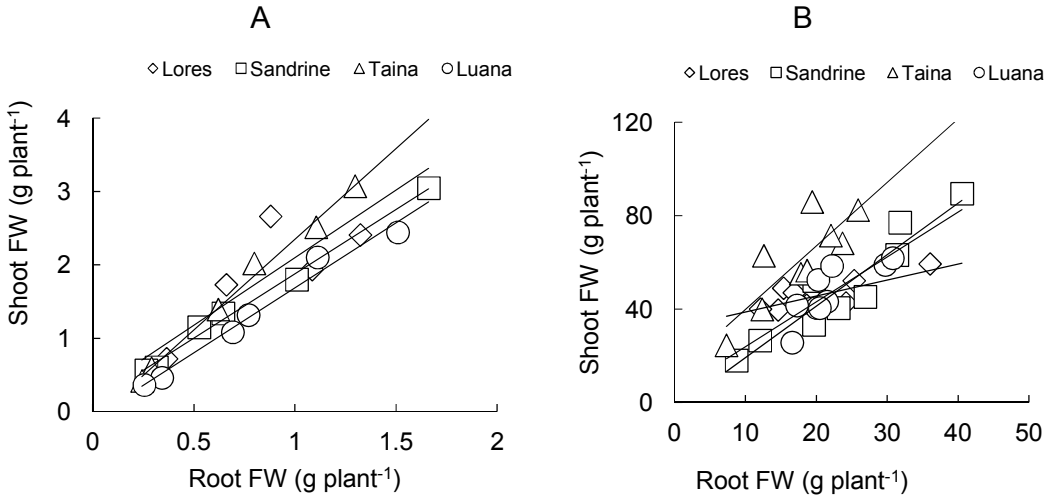


Fig. 4. Relationships between shoots and roots FW according to three plug cell volumes (50-, 128- and 288-cell tray^{-1}) for four lettuce plants at the transplant stage (A) (nursery experiment) and at the end of the pot experiments (B). The straight-line regression were: (A) Shoot FW_{Lores} = 1.84 Root FW + 0.25 (r^2 = 0.738; P < 0.001); Shoot $FW_{Sandrine}$ = 1.75 Root FW + 0.30 (r^2 = 0.992; P < 0.001); Shoot FW_{Taina} = 2.47 Root FW - 0.13 (r^2 = 0.993; P < 0.001Shoot FW_{Luana} = 1.77 Root FW - 0.09 (r^2 = 0.979; P < 0.001). (B) Shoot FW_{Lores} = 0.68 Root FW + 31.86 (r^2 = 0.672; P < 0.001); Shoot $FW_{Sandrine}$ = 2.20 Root FW - 2.80 (r^2 = 0.889; P < 0.001); Shoot FW_{Taina} = 2.72 Root FW + 12.59 (r^2 = 0.694; P < 0.001Shoot FW_{Luana} = 1.92 Root FW + 4.62 (r^2 = 0.661; P < 0.001)

3.2 Leaf Area Expansion

Both at the transplant stage (nursery experiment) and the end of the pot experiments lettuce plants significantly decreased total and individual leaf areas according to plug cell volume in the four lettuce genotypes tested. Plants BAP-sprayed decreased total and individual leaf areas when they were sprayed at the pre-transplant stage but increased both when they were sprayed at the post-transplant stage for the three plug cell volume tested (Table 1).

The higher plug cell volume the higher the rate of leaf appearance (RLA) and the relative leaf area expansion rate (RLAE) so at the transplant stage as at the pot experiments in control plants. A BAP spray at both pre- and post-transplant significantly increased RLA and RLAE (Table 2).

3.3 Dry Weight Accumulation

RGR values were significantly different from plants grown in different plug cell volume; data were higher in 50-cell trays than those grown in 128- or 288-cell trays as at the nursery as at the pot experiments. A pre- or post-transplant BAP spray significantly increased RGR over controls. When RGR was separating from their 'physiological' (NAR) and 'morphological' (LAR) components, we found that NAR decreased according plug cell volume decreased with a

significant increase in BAP-sprayed plants related to controls. NAR values were higher during the pot experiment than during the nursery ones. On the contrary, an inverse pattern for LAR was found. All lettuce genotypes tested showed a similar response to the same treatments (plug cell volume and BAP application) (Table 4).

Table 1. The effects of three plug cell volumes (50-, 128- and 288-cells tray^{-1}) and a pre- or post-transplant BAP spray (100 mg L^{-1}) on lettuce both total and individual leaf area at the transplant stage and the end of the experiments. Different lower case letters indicate significant differences (P < 0.05) between treatments. Different capital letters indicate significant differences (P < 0.05) between plants from different lettuce genotypes for the same treatment

	Leaf area (cm^2 plant^{-1})		Leaf area (cm^2 leaf^{-1})	
	Nursery	**Pot**	**Nursery**	**Pot**
Lores				
50-Control	115.48^{aA}	810.67^{cA}	14.11^{aA}	28.31^{cB}
50-BAP$_{Pre}$	84.60^{bA}	863.59^{bB}	6.04^{cD}	37.42^{dB}
50-BAP$_{Post}$		982.66^{aC}		38.83^{cB}
128-Control	79.26^{cA}	656.21^{fC}	9.88^{bB}	27.96^{dC}
128-BAP$_{Pre}$	51.73^{dA}	688.62^{eB}	3.98^{dB}	24.61^{fD}
128-BAP$_{Post}$		706.48^{dC}		26.70^{eC}
288-Control	22.41^{eA}	363.16^{iC}	3.68^{dA}	22.20^{aC}
288-BAP$_{Pre}$	16.74^{fB}	447.18^{hA}	2.09^{eB}	22.49^{gD}
288-BAP$_{Post}$		690.28^{gB}		30.26^{bB}
Sandrine				
50-Control	117.77^{aA}	674.05^{cC}	14.61^{aA}	23.09^{cC}
50-BAP$_{Pre}$	72.08^{bB}	885.05^{bB}	7.21^{aC}	30.38^{aC}
50-BAP$_{Post}$		1146.63^{aA}		30.20^{aC}
128-Control	58.69^{cB}	495.79^{fD}	7.17^{aC}	18.86^{dD}
128-BAP$_{Pre}$	33.72^{dB}	560.70^{eC}	3.75^{bB}	30.45^{aC}
128-BAP$_{Post}$		603.22^{dD}		21.02^{dD}
288-Control	22.17^{eA}	395.80^{gB}	3.68^{bA}	17.77^{eD}
288-BAP$_{Pre}$	15.92^{fB}	474.94^{fA}	1.99^{cB}	28.65^{bC}
288-BAP$_{Post}$		468.33^{fC}		15.03^{fD}
Taina				
50-Control	109.47^{aA}	833.99^{cA}	13.84^{aB}	48.87^{dA}
50-BAP$_{Pre}$	89.33^{bA}	905.32^{bA}	12.76^{cA}	47.05^{dA}
50-BAP$_{Post}$		1093.60^{aB}		45.06^{eA}
128-Control	74.20^{cA}	530.09^{fD}	14.79^{bA}	36.89^{gB}
128-BAP$_{Pre}$	49.60^{dA}	732.42^{eB}	6.20^{dA}	41.38^{fB}
128-BAP$_{Post}$		839.61^{dA}		57.75^{bA}
288-Control	19.13^{eA}	325.90^{gD}	4.03^{eA}	24.98^{hB}
288-BAP$_{Pre}$	20.30^{eA}	550.19^{fA}	3.06^{fA}	51.18^{cA}
288-BAP$_{Post}$		748.81^{eA}		60.98^{aA}
Luana				
50-Control	97.91^{aB}	709.33^{cB}	13.93^{aB}	49.53^{bA}
50-BAP$_{Pre}$	87.26^{bA}	827.59^{aC}	10.91^{bB}	48.62^{cA}
50-BAP$_{Post}$		783.17^{bA}		37.06^{fB}
128-Control	55.37^{cB}	542.90^{eC}	7.03^{cC}	40.03^{eA}
128-BAP$_{Pre}$	41.19^{dA}	780.17^{bB}	5.88^{dA}	52.35^{aA}
128-BAP$_{Post}$		578.75^{dA}		34.97^{gB}
288-Control	18.39^{eB}	557.08^{eA}	3.68^{eA}	43.69^{dA}
288-BAP$_{Pre}$	12.46^{fC}	542.09^{eA}	2.08^{fB}	43.02^{dB}
288-BAP$_{Post}$		344.09^{fD}		24.56^{hC}

Table 2. The effects of three plug cell volumes (50-, 128- and 288-cells tray^{-1}) and a pre- or post-transplant BAP spray (100 mg L^{-1}) on lettuce RLA and RLAE during both nursery and pot experiments. Different lower case letters indicate significant differences (P < 0.05) between treatments. Different capital letters indicate significant differences (P < 0.05) between plants from different lettuce genotypes for the same treatment

	RLA (leaves week^{-1})		RLAE (cm^2 cm^{-2} day^{-1})	
	Nursery	**Pot**	**Nursery**	**Pot**
Lores				
50-Control	1.250^{bA}	0.421^{bA}	0.0769^{aA}	0.0477^{aA}
50-BAP$_{Pre}$	1.338^{aA}	0.466^{bA}	0.0703^{bA}	0.0463^{aA}
50-BAP$_{Post}$		0.501^{aB}		0.0464^{aA}
128-Control	1.038^{dA}	0.349^{cA}	0.0675^{cA}	0.0421^{bA}
128-BAP$_{Pre}$	1.200^{cA}	0.412^{bA}	0.0718^{bA}	0.0450^{aA}
128-BAP$_{Post}$		0.394^{cA}		0.0477^{aA}
288-Control	0.800^{eA}	0.306^{eA}	0.0422^{dB}	0.0407^{bA}
288-BAP$_{Pre}$	0.838^{eB}	0.366^{dA}	0.0408^{dB}	0.0488^{aA}
288-BAP$_{Post}$		0.340^{dA}		0.0481^{aA}
Sandrine				
50-Control	1.200^{bB}	0.436^{bA}	0.0736^{aA}	0.0434^{bA}
50-BAP$_{Pre}$	1.325^{aA}	0.442^{bA}	0.0656^{bB}	0.0472^{aA}
50-BAP$_{Post}$		0.567^{aA}		0.0483^{aA}
128-Control	0.950^{dA}	0.388^{cA}	0.0620^{bB}	0.0422^{bA}
128-BAP$_{Pre}$	1.275^{cA}	0.457^{bA}	0.0573^{cC}	0.0488^{aA}
128-BAP$_{Post}$		0.427^{bA}		0.0442^{bA}
288-Control	0.888^{eA}	0.332^{dA}	0.0472^{dA}	0.0407^{cA}
288-BAP$_{Pre}$	1.050^{dA}	0.394^{cA}	0.0411^{eB}	0.0491^{aA}
288-BAP$_{Post}$		0.259^{eB}		0.0387^{cB}
Taina				
50-Control	0.763^{cC}	0.260^{bB}	0.0724^{aA}	0.0457^{aA}
50-BAP$_{Pre}$	0.900^{aB}	0.287^{bB}	0.0730^{aA}	0.0468^{aA}
50-BAP$_{Post}$		0.361^{aC}		0.0484^{aA}
128-Control	0.650^{dB}	0.212^{cB}	0.0674^{bA}	0.0421^{cA}
128-BAP$_{Pre}$	0.850^{bB}	0.263^{bB}	0.0674^{bB}	0.0456^{bA}
128-BAP$_{Post}$		0.291^{bB}		0.0494^{aA}
288-Control	0.675^{dB}	0.175^{dB}	0.0460^{cA}	0.0394^{cA}
288-BAP$_{Pre}$	0.700^{dC}	0.218^{cB}	0.0461^{cA}	0.0490^{aA}
288-BAP$_{Post}$		0.233^{cC}		0.0508^{aA}
Luana				
50-Control	0.813^{bD}	0.239^{bB}	0.0705^{aB}	0.0454^{aA}
50-BAP$_{Pre}$	0.913^{aB}	0.254^{bB}	0.0706^{aB}	0.0460^{aA}
50-BAP$_{Post}$		0.284^{aC}		0.0441^{aA}
128-Control	0.638^{cB}	0.200^{cB}	0.0601^{bB}	0.0425^{bA}
128-BAP$_{Pre}$	0.825^{bB}	0.224^{cB}	0.0597^{bC}	0.0471^{aA}
128-BAP$_{Post}$		0.245^{bB}		0.0438^{aB}
288-Control	0.625^{cB}	0.194^{dB}	0.0387^{cB}	0.0407^{cA}
288-BAP$_{Pre}$	0.663^{cD}	0.188^{dB}	0.0374^{cC}	0.0468^{aA}
288-BAP$_{Post}$		0.209^{cC}		0.0422^{bB}

Table 3. The effects of three plug cell volumes (50-, 128- and 288-cells tray^{-1}) and a pre- or post-transplant BAP spray (100 mg L^{-1}) on lettuce RGR, NAR and LAR at both nursery and pot experiments. Different lower case letters indicate significant differences (P < 0.05) between treatments. Different capital letters indicate significant differences (P < 0.05) between plants from different lettuce genotypes for the same treatment

	RGR (g g^{-1} day^{-1})		NAR (g cm^{-2} day^{-1}) x 10^{-5}		LAR (cm^2 g^{-1})	
	Nursery	**Pot**	**Nursery**	**Pot**	**Nursery**	**Pot**
Lores						
50-Control	0.0655^{bA}	0.0619^{bA}	19.37^{aC}	30.24^{bA}	338.12^{cA}	238.91^{bB}
50-BAP$_{Pre}$	0.0726^{aA}	0.0633^{aB}	16.27^{bB}	29.63^{cA}	446.21^{aA}	213.62^{cC}
50-BAP$_{Post}$		0.0641^{aB}		32.26^{aA}		198.68^{dC}
128-Control	0.0530^{bB}	0.0588^{cB}	16.52^{bA}	29.31^{cA}	350.73^{cB}	211.22^{cC}
128-BAP$_{Pre}$	0.0582^{aA}	0.0598^{cB}	13.75^{cC}	31.31^{bA}	423.22^{bA}	191.01^{dD}
128-BAP$_{Post}$		0.0643^{aB}		21.29^{eB}		302.05^{aC}
288-Control	0.0489^{aA}	0.0591^{cA}	13.91^{cA}	24.61^{dB}	351.64^{cB}	195.43^{dD}
288-BAP$_{Pre}$	0.0431^{bB}	0.0579^{dC}	12.85^{dA}	26.62^{dA}	335.36^{cD}	217.54^{cD}
288-BAP$_{Post}$		0.0596^{cC}		30.19^{bA}		197.39^{dC}
Sandrine						
50-Control	0.0646^{aB}	0.0716^{bA}	25.02^{aA}	23.76^{aB}	243.81^{dB}	521.76^{cA}
50-BAP$_{Pre}$	0.0522^{bC}	0.0762^{aA}	15.32^{bC}	13.75^{eC}	340.67^{cB}	554.35^{bA}
50-BAP$_{Post}$		0.0745^{aA}		12.18^{fD}		611.55^{aA}
128-Control	0.0610^{aA}	0.0608^{dA}	15.22^{bB}	16.05^{dB}	424.41^{aA}	255.90^{hB}
128-BAP$_{Pre}$	0.0519^{bB}	0.0693^{cA}	15.23^{bA}	22.27^{bC}	340.84^{cB}	311.19^{gA}
128-BAP$_{Post}$		0.0636^{dB}		23.53^{aA}		270.32^{hC}
288-Control	0.0504^{aA}	0.0600^{eA}	12.62^{cB}	13.72^{eD}	399.49^{bA}	374.50^{eB}
288-BAP$_{Pre}$	0.0519^{aA}	0.0705^{bB}	11.42^{dB}	17.20^{cB}	454.46^{aB}	409.81^{dC}
288-BAP$_{Post}$		0.0592^{eC}		17.43^{cB}		330.64^{fB}
Taina						
50-Control	0.0621^{aB}	0.0595^{eB}	21.66^{aB}	28.25^{bB}	286.66^{dB}	208.74^{hC}
50-BAP$_{Pre}$	$0,0627^{aB}$	0.0602^{eC}	19.20^{bA}	26.23^{cB}	326.59^{cB}	229.50^{gB}
50-BAP$_{Post}$		0.0626^{dB}		28.81^{aB}		217.30^{gB}
128-Control	$0,0565^{aB}$	0.0578^{eB}	14.64^{cC}	20.53^{dC}	385.95^{bA}	280.96^{eB}
128-BAP$_{Pre}$	$0,0531^{aB}$	0.0644^{cC}	13.35^{dC}	26.32^{cB}	397.70^{bA}	244.64^{fB}
128-BAP$_{Post}$		0.0701^{bA}		17.25^{eC}		406.34^{cA}
288-Control	$0,0374^{bB}$	0.0504^{fB}	8.90^{fD}	13.92^{gC}	420.06^{bA}	362.35^{dB}
288-BAP$_{Pre}$	$0,0514^{aA}$	0.0744^{aA}	9.47^{eD}	13.79^{gC}	543.05^{aA}	539.48^{aA}
288-BAP$_{Post}$		0.0740^{aA}		15.42^{fC}		479.96^{bA}
Luana						
50-Control	0.0620^{aB}	0.0612^{cB}	18.20^{aD}	29.80^{aA}	340.60^{aA}	205.39^{fC}
50-BAP$_{Pre}$	0.0619^{aB}	0.0645^{bB}	16.40^{bB}	26.36^{cB}	377.44^{aB}	244.69^{eB}
50-BAP$_{Post}$		0.0570^{dC}		27.76^{bC}		205.35^{fB}
128-Control	0.0394^{cC}	0.0560^{dB}	16.36^{bA}	16.43^{fD}	240.86^{bC}	340.77^{cA}
128-BAP$_{Pre}$	0.0542^{bB}	0.0663^{bC}	14.46^{cB}	21.32^{dD}	374.73^{aB}	310.94^{dA}
128-BAP$_{Post}$		0.0560^{dC}		16.22^{fD}		345.36^{cB}
288-Control	0.0411^{cB}	0.0492^{eB}	11.81^{dC}	12.29^{hD}	348.03^{aB}	400.21^{bA}
288-BAP$_{Pre}$	0.0384^{dC}	0.0718^{aB}	10.06^{eC}	14.34^{gC}	381.80^{aC}	500.55^{aB}
288-BAP$_{Post}$		0.0647^{bB}		18.32^{eB}		353.22^{cB}

At the end of the nursery experiments, total glucose showed higher values in plants from 50-cells than in the other plug cell volumes with a significant increase in BAP-sprayed plants. However, glucose accumulation in Luana genotype was quite lower than in the other three lettuce genotypes tested (Fig. 5).

3.4 Photo Assimilates Partitioning

Allometries from roots: shoots showed that the lower the plug cell volume the higher the β coefficients which indicate that photo assimilates would be partitioned preferably to roots in both experiments (nursery and pot)

for control plants. A single pre- or post- BAP spray increased photo assimilates partitioning to shoots (lowered β coefficients) (Table 4).

Table 4. Changes in allometric relationships between roots and shoots for seedlings of four lettuce genotypes grown at three plug cell volumes (50-, 128- and 288-cells tray^{-1}) and sprayed with a pre- or post-transplant BAP (100 mg L^{-1}). Different lower case letters indicate significant differences (P < 0.05) between treatments. Different capital letters indicate significant differences (P < 0.05) between plants from different lettuce genotypes for the same treatment

	β	
	Nursery	**Pot**
Lores		
50-Control	0.78^{bA}	0.89^{cB}
50-BAP_{Pre}	0.62^{cA}	0.80^{fB}
50-BAP_{Post}		0.85^{dB}
128-Control	0.73^{bB}	0.91^{bD}
128-BAP_{Pre}	0.62^{cB}	0.86^{dC}
128-BAP_{Post}		0.82^{eD}
288-Control	0.88^{aA}	0.954^{aB}
288-BAP_{Pre}	0.68^{cA}	0.91^{bC}
288-BAP_{Post}		0.91^{bC}
Sandrine		
50-Control	0.71^{bA}	0.97^{dA}
50-BAP_{Pre}	0.67^{cA}	0.94^{eA}
50-BAP_{Post}		0.94^{eA}
128-Control	0.87^{aA}	0.99^{cA}
128-BAP_{Pre}	0.75^{bA}	0.94^{eA}
128-BAP_{Post}		0.97^{dA}
288-Control	0.77^{bB}	1.06^{aA}
288-BAP_{Pre}	0.70^{bA}	1.05^{aA}
288-BAP_{Post}		1.00^{bA}
Taina		
50-Control	0.69^{bA}	0.81^{cC}
50-BAP_{Pre}	0.43^{dB}	0.78^{dC}
50-BAP_{Post}		0.81^{cC}
128-Control	0.76^{aB}	0.96^{aB}
128-BAP_{Pre}	0.56^{cB}	0.89^{bB}
128-BAP_{Post}		0.94^{aB}
288-Control	0.76^{aB}	0.89^{bC}
288-BAP_{Pre}	0.53^{cB}	0.88^{bD}
288-BAP_{Post}		0.89^{bB}
Luana		
50-Control	0.74^{aA}	0.88^{dB}
50-BAP_{Pre}	0.62^{bA}	0.80^{eB}
50-BAP_{Post}		0.81^{eC}
128-Control	0.77^{aB}	0.94^{bC}
128-BAP_{Pre}	0.67^{bB}	0.93^{bA}
128-BAP_{Post}		0.94^{bB}
288-Control	0.85^{aA}	0.97^{aB}
288-BAP_{Pre}	0.63^{bA}	0.91^{cB}
288-BAP_{Post}		0.91^{cB}

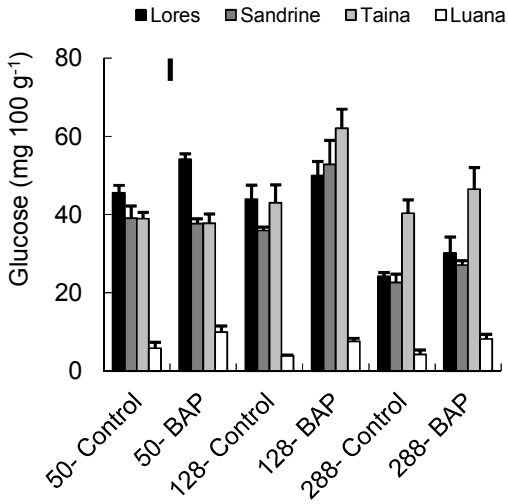


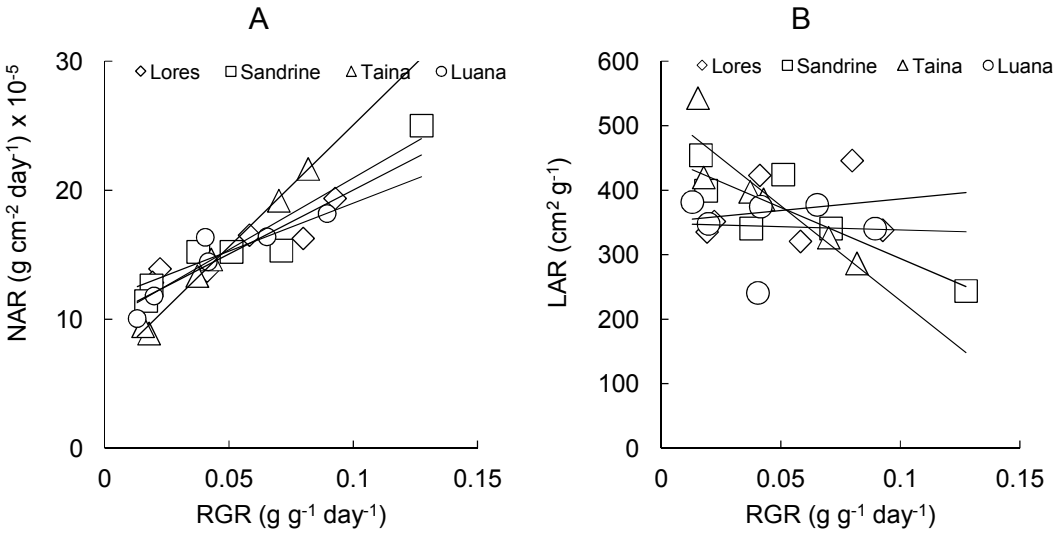
Fig. 5. The effects of three plug cell volumes (50-, 128- and 288-cells tray^{-1}) and a pre-transplant BAP spray (100 mg L^{-1}) on glucose content at the end of the nursery experiments for four lettuce genotypes. Vertical lines on bars indicate standard errors and vertical line indicate least significant differences (LSD)

3.5 Growth Parameters Relationships

When plotting the data from all treatments, we found a close direct relationship between RGR and NAR for all lettuce genotypes tested (Fig. 6A) and an inverse relationship between RGR and LAR (Fig. 6B) during nursery. On the other hand, during the pot experiments, NAR and LAR (Fig. 6C and D) were mainly positively correlated with RGR.

During nursery, positive relationships between RLAE (Fig. 7A), RLA (Fig. 7B), RGR (Fig. 7C), NAR (Fig. 7D), glucose content (Fig. 7E) and root dry weight were found, with minor quantitative differences between lettuce genotypes.

In the same way, positive relationships between RLAE (Fig. 8A), RLA (Fig. 8B), RGR (Fig. 8C), NAR (Fig. 8D) and root dry weight were found during the pot experiments.



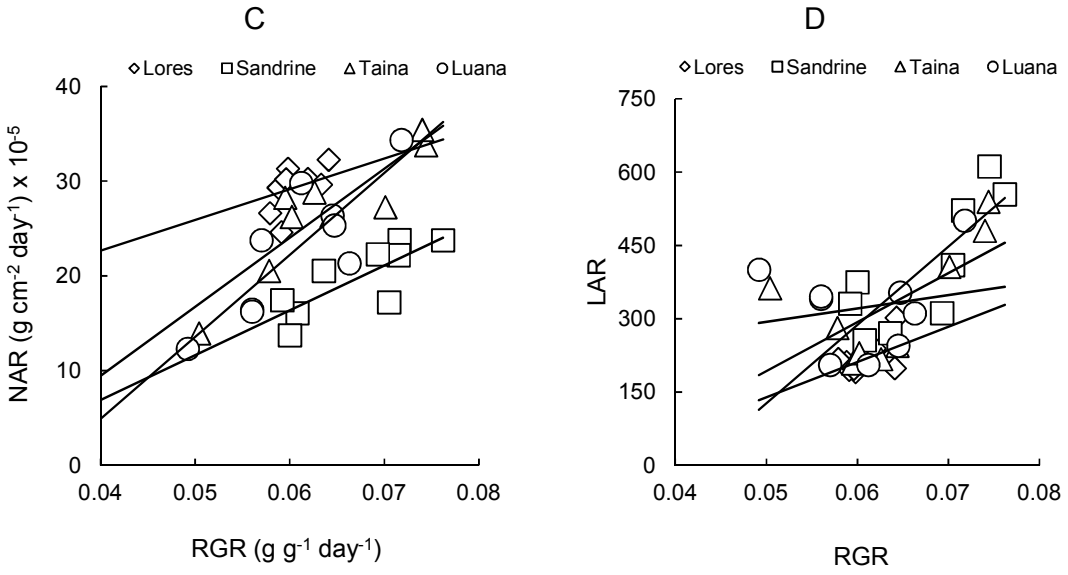
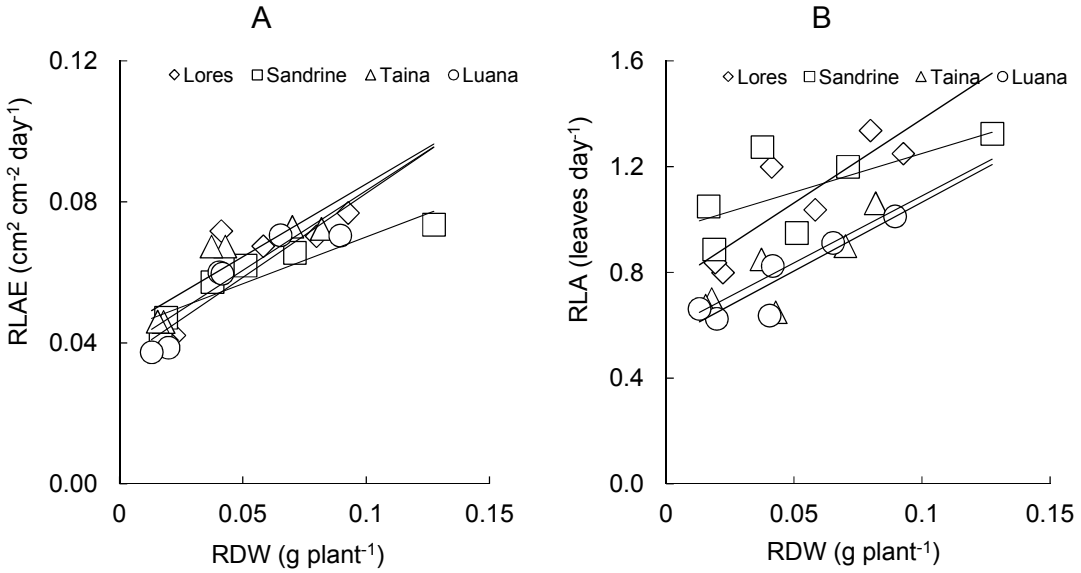


Fig. 6. Relationships between NAR (A, C), LAR (B, D) and RGR according to four lettuce genotypes grown at three plug cell volumes (50-, 128- and 288-cells tray^{-1}) and a pre- or post-transplant BAP sprays (100 mg L^{-1}) at both transplant stage (A, B) and the end of experiments (C, D). The straight-line regressions were, $NAR_{Lores\text{-}transplant}$ = 74.51 RGR + 11.56 (r^2 = 0.862; P < 0.001); $NAR_{Sandrine\text{-}transplant}$ = 111.22 RGR + 9.83 (r^2 = 0.923; P < 0.001); $NAR_{Taina\text{-}transplant}$ = 189.01 RGR + 6.19 (r^2 = 0.994; P < 0.001); $NAR_{Luana\text{-}transplant}$ = 99.33 RGR + 10.09 (r^2 = 0.841; P < 0.001); $LAR_{Lores\text{-}transplant}$ = 358.72 RGR + 350.49 (r^2 = 0.043); $LAR_{Sandrine\text{-}transplant}$ = -1588,40 RGR + 452.63 (r^2 = 0.759; P < 0.001); $LAR_{Taina\text{-}transplant}$ = -2945.40 RGR + 523.42 (r^2 = 0.813; P < 0.001); $LAR_{Luana\text{-}transplant}$ = -102.44 RGR + 348.51 (r^2 = 0.003). $NAR_{Lores\text{-}end}$ = 324.54 RGR + 9.68 (r^2 = 0.681; P < 0.001); $NAR_{Sandrine\text{-}end}$ = 473.33 RGR + 12.04 (r^2 = 0.637; P < 0.001); $NAR_{Taina\text{-}end}$ = 729.20 RGR + 19.73 (r^2 = 0.801; P < 0.001); $NAR_{Luana\text{-}end}$ = 866.00 RGR – 29.73 (r^2 = 0.706; P < 0.001); $LAR_{Lores\text{-}end}$ = 7216.00 RGR – 221.59 (r^2 = 0.261); $LAR_{Sandrine\text{-}end}$ = 16061.00 RGR – 676.47 (r^2 = 0.651; P < 0.001); $LAR_{Taina\text{-}end}$ = 10021.00 RGR + 308.54 (r^2 = 0.421; P < 0,001); $LAR_{Luana\text{-}end}$ = 2734.90 RGR + 156.81 (r^2 = 0,038)



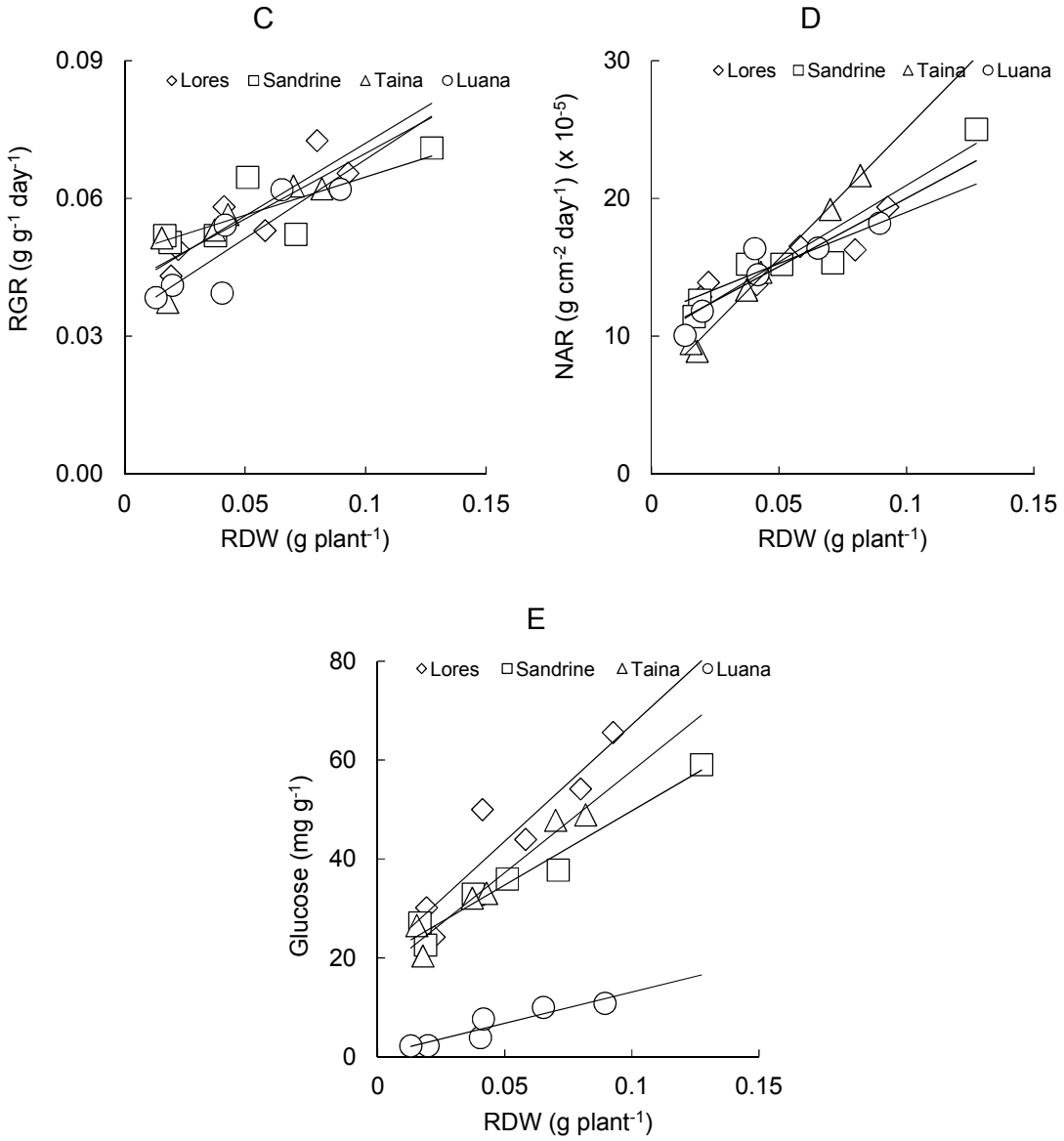


Fig. 7. Relationships between RLAE (A), RLA (B), RGR (C), NAR (D), glucose content (E) and root dry weight (RDW) for four lettuce genotypes grown at three plug cell volumes (50-, 128- and 288-cells tray^{-1}) and a pre- or post-transplant BAP sprays (100 mg L^{-1}) at the transplant stage. The straight-line regressions were, $RLAE_{Lores}$ = 0.45 RDW + 0.044 (r^2 = 0.736; P < 0.001); $RLAE_{Sandrine}$ = 0.27 RDW + 0.038 (r^2 = 0.845; P < 0.001); $RLAE_{Taina}$ = 0.41 RDW + 0.044 (r^2 = 0.783; P < 0.001); $RLAE_{Luana}$ = 0.48 RDW + 0.035 (r^2 = 0.840; P < 0.001); RLA_{Lores} = 6.34 RDW + 0.75 (r^2 = 0.735; P < 0.001); $RLA_{Sandrine}$ = 2.93 RDW + 0.96 (r^2 = 0.604; P < 0.001); RLA_{Taina} = 5.07 RDW + 0.58 (r^2 = 0.727; P < 0.001); RLA_{Luana} = 5.20 RDW + 0.55 (r^2 = 0.835; P < 0.001); RGR_{Lores} = 0.32 RDW + 0.04 (r^2 = 0.772; P < 0.001); $RGR_{Sandrine}$ = 0.17 RDW + 0.05 (r^2 = 0.639; P < 0.001); RGR_{Taina} = 0.29 RDW + 0.04 (r^2 = 0.694; P < 0.001); RGR_{Luana} = 0.35 RDW + 0.03 (r^2 = 0.770; P < 0.001); NAR_{Lores} = 74.51 RDW + 11.55 (r^2 = 0.862; P < 0.001); $NAR_{Sandrine}$ = 111.22 RDW + 9.82 (r^2 = 0.923; P < 0.001); NAR_{Taina} = 189.01 RDW + 6.19 (r^2 = 0.994; P < 0.001); NAR_{Luana} = 99.33 RDW + 10.09 (r^2 = 0.841; P < 0.001); $Glucose_{Lores}$ = 470.78 RDW + 20.10 (r^2 = 0.849; P < 0.001); $Glucose_{Sandrine}$ = 300.51 RDW + 19.73 (r^2 = 0.963; P < 0.001); $Glucose_{Taina}$ = 412.35 RDW + 16.59 (r^2 = 0.947; P < 0,001); $Glucose_{Luana}$ = 126.48 RDW + 0.44 (r^2 = 0.872; P < 0.001)

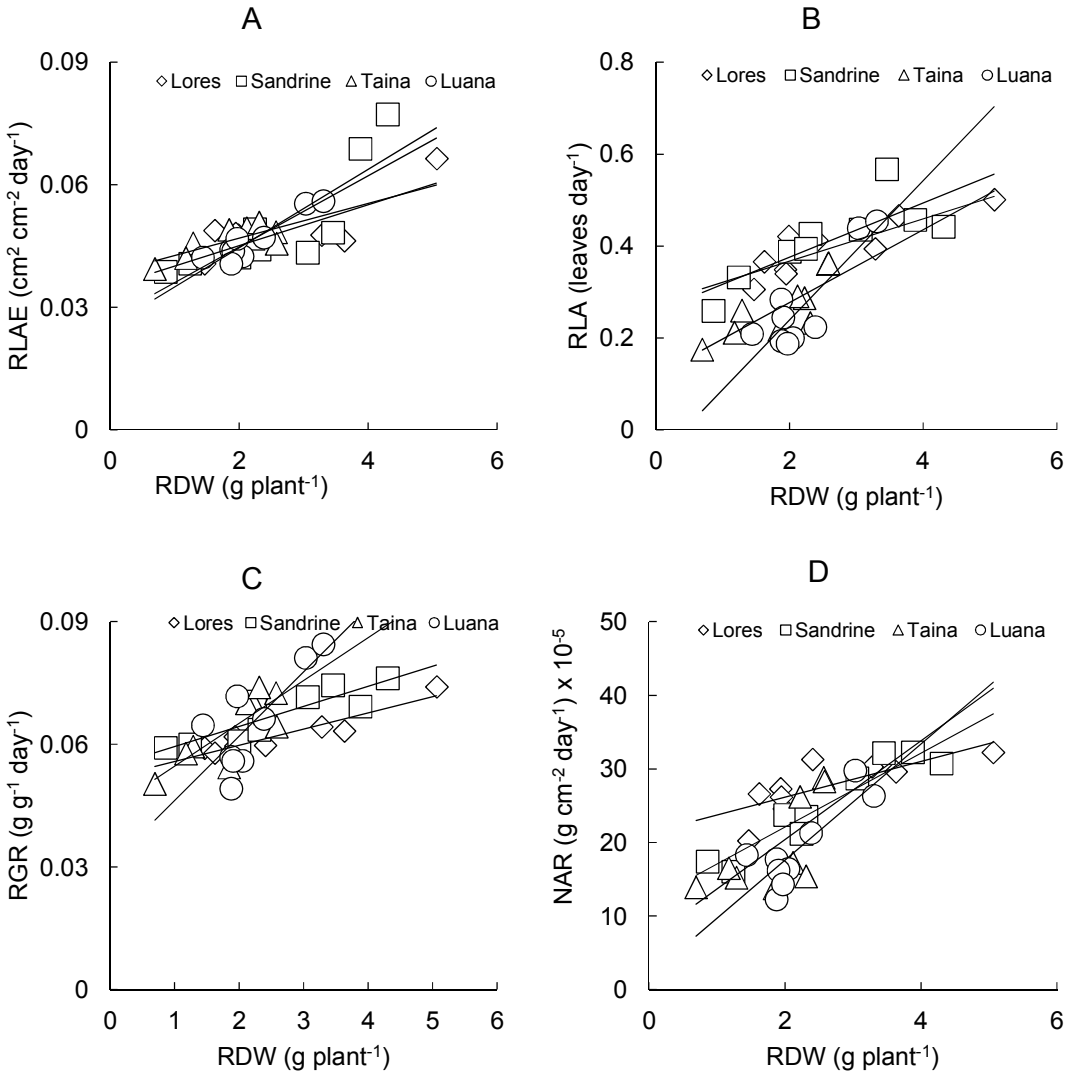


Fig. 8. Relationships between RLAE (A), RLA (B), RGR (C), NAR (D) and root dry weight (RDW) for four lettuce genotypes grown at three plug cell volumes (50-, 128- and 288-cells tray^{-1}) and a pre- or post-transplant BAP sprays (100 mg L^{-1}) at the end of the experiment. The straight-line regressions were, $RLAE_{Lores}$ = 0.005 RDW + 0.035 (r^2 = 0.630; P < 0.001); $RLAE_{Sandrine}$ = 0.010 RDW + 0.025 (r^2 = 0.695; P < 0.001); $RLAE_{Taina}$ = 0.004 RDW + 0.038 (r^2 = 0.600; P < 0.001); $RLAE_{Luana}$ = 0.009 RDW + 0.027 (r^2 = 0.877; P < 0.001); RLA_{Lores} = 0.046 RDW + 0.28 (r^2 = 0.752; P < 0.001); $RLA_{Sandrine}$ = 0.059 RDW + 0.26 (r^2 = 0.649; P < 0.001); RLA_{Taina} = 0.08 RDW + 0.12 (r^2 = 0.659; P < 0.001); RLA_{Luana} = 0.15 RDW – 0.06 (r^2 = 0.768; P < 0.001); RGR_{Lores} = 0.004 RDW + 0.05 (r^2 = 0.875; P < 0.001); $RGR_{Sandrine}$ = 0.005 RDW + 0.05 (r^2 = 0.779; P < 0.001); RGR_{Taina} = 0.01 RDW + 0.04 (r^2 = 0.674; P < 0.001); RGR_{Luana} = 0.02 RDW + 0.03 (r^2 = 0.616; P < 0.001); NAR_{Lores} = 2.42 RDW + 21.33 (r^2 = 0.578; P < 0.001); $NAR_{Sandrine}$ = 5.02 RDW + 12.09 (r^2 = 0.897; P < 0.001); NAR_{Taina} = 6.71 RDW + 6.99 (r^2 = 0.601; P < 0.001); NAR_{Luana} = 7.89 RDW + 1.83 (r^2 = 0.700; P < 0.001)

4. DISCUSSION

The root restriction related to limited plug cell volume has been defined as a physical stress imposed on the root system when plants are grown in small containers and leads to a pronounced decrease in both root and shoot growth of the plants both at the transplant stage and during field growth cycle [1].

Based on the assumption that the plant responses to this abiotic stress is mainly associated with a negative hormonal signaling from roots, we have proposed that this stress would be overridden by using a pre-transplant spray of BAP, a synthetic cytokinin able to regulate plant metabolism [4,10]. BAP can be considered an endogenous-like compounds which implies very little risk to the environment, because it is not toxic to several important mite predator species used for the biological control of phytophagous mites and because its toxicity to mammalian and arthropod species is low. However, the implementation of commercial applications of BAP in vegetables is still a pending issue.

Plant growth is the result of leaf area expansion, photo-assimilate acquisition and partition which, finally determine both absolute fresh-dry weight accumulations and growth rates. A limited plug cell volume, decreased all these traits during nursery but the negative effects remain during field growth. Previous data from our laboratory showed that this response appears alike in different vegetables such as lettuce and celery [7,11,12], spinach [13,14], Butternut squash [15] and tomato [16]. Different plug cell volume has been tested (288-, 200- and 128- plug cell traits) and values decreased according plug cell volume decreased. A single BAP spray when the first true leaf pair was developed, increased responses in all plug cell volume previously tested.

When the same BAP dose is applied after transplant, usually fall to stimulate the responses and plants from the higher cell volume significantly decreased their biomass accumulation. We would speculate that the decreased responses under limited root growth would stablish an insufficient endogenous cytokinin level, which negatively would regulate plant growth. When a BAP spray is used, the effective cytokinin concentration at the shoot apical meristem would be increased near the optimum, explained by the positive growth responses. But, when seedlings are transplanted to the field or a higher pot, roots expanded until a new limiting factor appears. At the same time, roots growth in large but they branch it and the endogenous cytokinin level increased as well. At this moment, an exogenous BAP spray over-increased cytokinin level at the shoot apical meristem and a negative growth signal is happened. In this work, we used 50-plug cell traits, an unusual plug cell volume from vegetable commercial nurseries. For control plants, the higher fresh-dry weight (Figs. 1 and 2), total leaf areas (Table 1) and growth rates (Tables 2 and 3) was found at both nursery and pot experiments. At the same time, a BAP spray gives a decrease in all these traits, which support the previous hypothesis.

A second novelty result from this work is found in Fig. 3, where significant size differences can be seen in plants at the transplant stage (at the end of nursery experiments) to pots. The initial non-limited space at this time changes whenever roots spread out and take up the pot. At this time, a new root restriction is happened and shoot growth decreased. Poorter et al. [17] indicated that the appropriate pot size will logically depend on the size of the plants growing in them, although they suggested that an appropriate pot size is one in which the plant biomass does not exceed 1 g L^{-1}. In current research practice, about 65% of the experiments, exceed that threshold and let to explain the results from Fig. 3. Anyway, our results confirm previous reports and do not disallow qualitative conclusions.

One of the main objectives from this work was testing the response of different lettuce genotypes. On account of this, two butter heads and two crisp head lettuce with different environment requirement was included. The butter head Lores is seeded and growth during spring, summer and autumn, while the butter head Sandrine is suggested for growing during autumn and winter. On the other hand, Taina and Luana are crisp head lettuce; the first is particularly suited for warm season production while Luana is sowed during autumn and winter. Our results indicated, with minor quantitative differences, that all lettuce genotypes showed the same response pattern to both limit plug cell volume and BAP application responses.

Plant growth implies the acquisition of assimilates from photosynthesis. Therefor initiation and maintenance of organs related to light interception (stems and leaves), water and nutrient absorption (roots) is needed. On the other hand, the balanced root: shoot ratio required photo assimilates partition, which can be modified as by environmental traits as by endogenous hormonal balance. To support this assumption Fig. 4 showed that shoot growth is significantly correlated by root growth. In the same way, Figs. 7 and 8 displayed positive significant correlations between RLAE, RLA, RGR, NAR, glucose content and root DW as

during nursery as during pot experiments. On the other hand, plant allometries between roots and shoots let to clearly suggest a higher photo assimilates partitioning to shoots in plants with higher roots systems (less root restrictions) and BAP-sprayed ones (Table 4), in agreement with Arkhipova et al. [18] who showed that accumulation of zeatin and its riboside was greatest in roots shortly two days after inoculation with bacteria inoculation.

Further analysis of pot size effects on the underlying components of growth by several authors [17,19,20] suggests that reduced growth in smaller pots is caused mainly by a reduction in photosynthesis per unit leaf area, rather than by changes in leaf morphology or biomass allocation. Our results showed a decrease in NAR (a photosynthesis capacity estimator) and glucose content (Fig. 5) under limited plug cell volume in all lettuce genotypes tested. In agreement with Poorter et al. [17], nursery results from Fig. 6 showed that RGR was mainly related to NAR, however, during pot experiments RGR was related both NAR and LAR.

Biomass accumulation is positively correlated to root restriction during both nursery and pot experiments (Figs. 1 and 2, Table 1) as in absolute terms as by growth rates (Tables 2 and 3). However, while a BAP spray decreased fresh-dry weight and leaf area, all these traits were increased during the pot experiments. The disagreement between these two data sets would be explained by the higher RLA in BAP-sprayed plants (Table 2) which must be supported by a high glucose content [21] a limited resource during nursery when seedlings have been developed a little leaf area.

5. CONCLUSIONS

From the physiological mechanisms involved, the higher biomass accumulation in lettuce plants non root-limited and BAP-sprayed ones are supported by higher photosynthetic rates, by higher leaf number initiation and expansion and by photo assimilate partition to shoots. Understanding the plant responses to this hormonal manipulation and the physiological mechanism involved will allow adjusting the agronomic advice for different vegetables and reaching to maximum commercial yields in each of them.

From the grower´s point of view, higher yields would be reached decreasing root restriction during nursery or with BAP-sprayed plants, but the accurate plug cell trait used, BAP concentration applied or time BAP application must be carefully calibrated for each vegetable for avoiding potentially negative results.

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COMPETING INTERESTS

Authors have declared that no competing interests exist.

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