Roots Partially Drive Super Sweet Maize Yield

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Authors' contributions

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

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ABSTRACT

Although it has been indicated that corn biomass accumulation between sowing and harvest are directly related to incident photosynthetically active radiation (PAR) intercepted by the canopy, plant roots can sense soil environment and, via some internal signal, transmit the condition of the soil to extending leaves. Experiments combined two plant densities, a transplant routine and a single benzyl aminopurine (BAP) spray on different super sweet maize hybrids to test the hypothesis that a changes in both light and root environments drive super sweet maize yield. Pot experiment showed a close coordination between roots and shoot growth while field experiments support the proposed hypothesis through the positive relationships between RLAE, CGR and yield and root dry weight. This novelty approach would indicate that root growth could be considered as a limiting factor to shoot growth and yield in super sweet maize crops.

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1. INTRODUCTION

Corn (*Zea mays)* popularity as a crop is largely due to its diverse functionality as a food source for both humans and animals [1]. It is truly staggering to discover the domination of corn in the American food system [2]. According to Pollan [3], more than one quarter of the 45,000 items found in an average American supermarket contain corn. Sweetness, good germination and high yield are important trait for sweet corn. Various recessive mutants in corn expressed in the endosperm, improve sweetness. In single mutant hybrids, the sugar concentration in sugary (*su1*) and *shrunken2* (*sh2*) corn is three and eight times than wild type respectively [4]. Sugary and sugary enhancer (*se*) hybrids are two of the most common types of sweet corn cultivated in temperate areas [5]. Super-sweet maize (*sh2*) is less well adapted to cold conditions [6], but maintained their eating quality for longer time after harvest than standard sweet corn hybrids [7]. Although previous reports have shown that super-sweet hybrids and inbreeds have lower emergence and lower early seedling vigor (particularly in cold conditions) than standard sweet hybrids [8,9,10], this trait would be partially overtake in most of the new hybrids [11,12,13].

Andrade et al. [14] indicated that corn biomass accumulation between sowing and harvest are directly related to incident photosynthetically active radiation (PAR) intercepted by the canopy, and from the efficiency with which the intercepted PAR is converted into dry matter. Leaf area strongly influences crop growth and the green leaf area development during the growing season is a fundamental component of crop growth [15]. Because radiation would be the key driving force in the ideal growth environment [16], such as ample available water, fertile soil and disease-free, three important indices must be considered such as, the fraction of radiation intercepted or light interception, the radiation use efficiency (RUE) and the harvest index (HI).

Grain formation in maize is the result of the photosynthetic ability of source leaves and the integrated process of allocation, accumulation and utilization of assimilated carbon at the whole plant level [17]. During development, the architecture of the stand depends on the growth pattern of individual plants, which leads to differences in the distribution of radiation within the stand. In turn, it may be responsible for differences in productivity indices per unit area, especially when a transplant routine significantly changes maize plant morphology [18] and ensures population stand.

Williams [19,20] has indicated that populations for maximum sweet corn yield vary greatly depending of the hybrid, ranging from 43,000 to 86,000 plants ha^{-1}. Although it has been indicated that transplant decreases sweet maize yield [21], we have previously found that yield (g fresh weight plant^{-1}) was not significantly different between direct-seeded and transplanted plants grown at low or high populations [12,18]. A detailed analysis of the effect of plant population density on sweet corn is scarce in the peer-reviewed literature but Rattin et al. [22] showed that plant density would be increase as far as 120.000 plants ha^{-1} when transplants was used.

Plant roots can sense adverse soil conditions and, via some internal signal, transmit the condition of the soil to extending leaves [23]. Rahayu et al. [24] indicated that a decrease in cytokinin supply from the root to the shoot might inhibit leaf growth. Endogenous cytokinins synthesized in roots are transported into shoots via the xylem [25], but controlled both by environmental and endogenous signals [26]. Kotov and Kotova [27] indicated that the higher the root system the higher the cytokinin-ribosides synthesized. Previous report [28,29,30,31] showed, in ornamental pot plants, a close relationship between shoot and root fresh-dry weights.

The aim of this work was to determine the combined effects of two plant densities, a transplant routine and a single benzyl aminopurine (BAP) spray on commercial yield for different super sweet maize hybrids to test the hypothesis that a changes in both light and root environments driven super sweet maize yield.

2. MATERIALS AND METHODS

2.1 Plant Material and Experiments

To reach proposed objectives and validate proposed hypothesis, two experiments were performed:

2.1.1 Experiment 1

A greenhouse experiment was carried out at the Faculty of Agronomy, University of Buenos Aires, Argentina (34° 35' 59''S, 58° 22' 23''W) during December 2013.

Four maize super sweet hybrids (*sh2*) ('1441', '3475', 'Vikingo' and 'Butter TR') with yields ranged between 15 to 17 ton ha^{-1} were provided by Semillería Basso (Argentina). Seeds were sown in plastic plug trays (128 cells tray^{-1}; 17.37 cm^3 cell^{-1}) using a commercial growing media (Klasmann 411® medium, Klasmann-Deilmann, GmbH, Germany) or direct-seeded in 5-litre pots filled with a *Sphagnum maguellanicum*-river waste-perlite (40-40-20, v/v/v) medium [32]. The plants were arranged at a density of 4 plants m^{-2}, which avoided mutual shading and both direct-seeded and transplants were at the same growth state at the beginning of the experiment.

Seedlings were sprayed with two BAP (6-benzylaminopurine) (SIGMA EC 214-927-5) (Sigma-Aldrich Co., St. Louis, MO, USA) solutions (0 and 50 mg l^{-1}) when first true leaf pairs appeared. BAP was previously diluted in alcohol 80% and plants were run-off sprayed.

At the beginning of the experiment total porosity (%), air-filled porosity (%), container capacity (%) and bulk density (g cm^{-3}) were 63.50, 17.06, 40.06 and 0.35 respectively. Organic matter (%), pH, electric conductivity (dS m^{-1}) and cation exchange capacity were 45.3, 5.2, 0.71 and 58.9 respectively. Seedlings were sprayed with two concentrations (0 and 50 mg l^{-1}) of BAP (one week after emergence.

A weekly ferti-irrigation of 1.0: 0.5: 1.0: 0.5 (v/v/v/v) N: P: K: Ca (nitric acid, phosphorus acid, potassium nitrate, and calcium nitrate) (150 mg l^{-1} N) was included through to the overhead irrigation water.

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. Minimum temperature, maximum temperature and mean global solar radiation during the experiment were 25.11°C, 28.31°C and 25.60 MJ m^{-2} day^{-1} respectively.

2.1.2 Experiment 2

The experiment was conducted at the INTA Balcarce Experimental Station, Argentina (37°45'S, 58°18'W) from 7th November 2012 to 7th February 2013 on a Typic Argiudoll soil with an organic matter of 5.6% in the first 25 cm depth. The experiment was repeated from 11th November 2014 to 14th February 2015. Water and nutrients were at non-limiting levels using an irrigation system, which kept soil water above 50% of maximum soil available water in the first meter of depth. The experimental field was fertilized with 150 kg N ha^{-1} (18-46-0) at the beginning of experiments. Weeds and insects were adequately controlled.

Three super sweet maize hybrids (*sh2*) ('1441', 'Vikingo' and 'Butter TR') provided by Semillería Basso (Argentina) were sown in plastic plug trays (128 cells tray^{-1}; 17.37 cm^3 cell^{-1}) using a commercial growing media (Klasmann 411® medium, Klasmann-Deilmann, GmbH, Germany) or direct-seeded. Transplanted plants were grown under greenhouse facilities from sowing to transplant and were conducted by hands. Both direct-seeded and transplants were at the same growth state at the beginning of the experiment. Final population densities were 40,000 and 80,000 plants ha^{-1}.

Water and nutrients were at non-limiting levels using an irrigation system, which kept soil water above 50% of maximum soil available water in the first meter of depth.

Seedlings were sprayed with BAP solutions (0 and 50 mg l^{-1}) when first true leaf pairs appeared. BAP was previously diluted in alcohol 80%.

Weather records (daily maximum-minimum air temperature and global solar radiation) were recorded from a meteorological station 500 meters from the experimental site. The air temperatures ranged between 10.60 to 14.45°C (minimum) and between 24.90 to 28.46°C (maximum) during the 2012-2013 experiment and between 10.87 to 14.06°C (minimum) and between 23.40 to 28.46°C (maximum) during the 2014-2015 experiment. Light ranged between 20.57 to 22.37 MJ m^{-2} day^{-1} and between 19.00 to 23.04 MJ m^{-2} day^{-1} during the 2012-2013 and 2014-2015 experiments respectively.

2.3 Growth Evaluations

2.3.1 Experiment 1

Plants for destructive measurements were harvested (five per treatment and block) at emergence and at 7-day intervals during the experiment. 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

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area was determined using a leaf area meter LI-COR FL16 (LI-COR Inc., Lincoln, NE, USA).

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 *vs.* time (in days) [33]. The rate of leaf area expansion (RLAE) was calculated as the slope of the regression of the ln of total leaf area *vs.* time (in days) [34]. The mean net assimilation rate (NAR), and the leaf area ratio (LAR) [35] 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); W_0: extrapolated value of total dry weight at time zero (g); A_0: extrapolated value of leaf area at time zero (cm^2); k_a: RLAE (days); t: time (days) at the midpoint of the experimental period and e: base of natural logarithms.

The specific leaf area on a FW basis (SLA) was calculated as the ratio between the area of the new individual leaf and leaf FW [36].

The allometric coefficients between root and shoot and between leaf blades and the petiole + stem fraction 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) and between the ln of the leaf blade DW *vs.* the ln of the petiole + stem DW (ln leaf blade DW = a **+** b x ln petiole + stem DW) respectively [37].

2.3.2 Experiment 2

For field experiments five plants per treatment at E-T (emergence-transplant) and V_4, V_7, V_9, V_T and R_3 stages were harvest. 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℃ for 96 hours. Individual leaf area was determined using a leaf area meter LI-COR FL16 (LI-COR Inc., Lincoln, NE, USA). The sample size was five plants per block. Leaf area index (LAI) was calculated using the total leaf area per unit sample soil.

The crop growth rate (CGR) related the total DW with time (days) and the unit sample soil (m^2) [38].

Photosynthetic active radiation (PAR) interception percentage was calculated as [1-(I_t/I_o)] x 100, where It is incident PAR just above the lowest layer of photosynthetically active leaves, and Io is incident PAR at the top of the canopy. The values for I_t and I_o were obtained with a LI-COR 188 B radiometer (LI-COR Inc, Lincoln, NE, USA) connected to a line quantum sensor LI-COR 191 SB. The measurements were confined to midday (11.30-13.00 hours) and taken on sunny days only. We carried out five measurements per block. Daily total incident PAR was multiplied by the corresponding daily fraction of PAR interception and accumulated to obtain the PAR intercepted by the crop from sowing to harvest [39]. Radiation use efficiency (RUE) was calculated as the dry matter accumulated divided by the intercepted PAR accumulated from E/T to V_T [40]. The harvest index (HI) was calculated as the FW of the harvested ears as a percentage of the total shoot FW of the plants [41].

2.4 Statistical Analysis

We used a complete aleatory design for Experiment 1 and a randomized design with three blocks of four rows of 10 m (0.70 m apart) for each treatment for Experiment 2. Since we found no significant differences in Experiment 2 data between two successive years, we considered them together (n = 6). Data were subjected to one-way analysis of variance and means were separated by Tukey's test (P < 0.05); STATISTICA 8 (StatSoft) software was used. Slopes from straight-line regressions of RLA, RLAE, RGR, NAR, LAR and allometric values were tested using the SMATR package [42].

3. RESULTS

3.1 Pot Experiment

Direct-seeded super sweet maize plants (Fig. 1A) showed higher fresh weight than transplanted ones (B) all experiment long. Although total fresh weight was not the same for different the maize hybrids, a BAP spray decreased it in control plants regardless of the hybrid tested. Transplants did not show

significant differences between controls and BAP-sprayed plants.

Transplants showed lower RLA and RLAE values than direct-seeding plants in all of the super sweet maize hybrids tested. No significant differences in SLA were found. A single BAP spray did not change RLA and RLAE (Table 1).

Control direct-seeded plants showed higher RGR and NAR values than transplanted controls. A single BAP application decreased or did not give significant changes. Anyway, direct seeded-BAP sprayed plants given higher RGR and NAR than transplanted-BAP sprayed ones. Only small but no significant differences in LAR were found in the most super sweet maize hybrids sowing by transplant or direct-seeded and sprayed or not with a single BAP.

Direct seeding control plants showed higher root: shoot and lower stems:leaves slope straight-line coefficients (β) than transplanted plants. A single BAP spray increased root: Shoot β coefficient in direct-seeded plants but decreased values in transplanted ones. On the other hand, stems: leaves β coefficients did not change in BAP-sprayed plants regardless of the cropping system (Table 3).
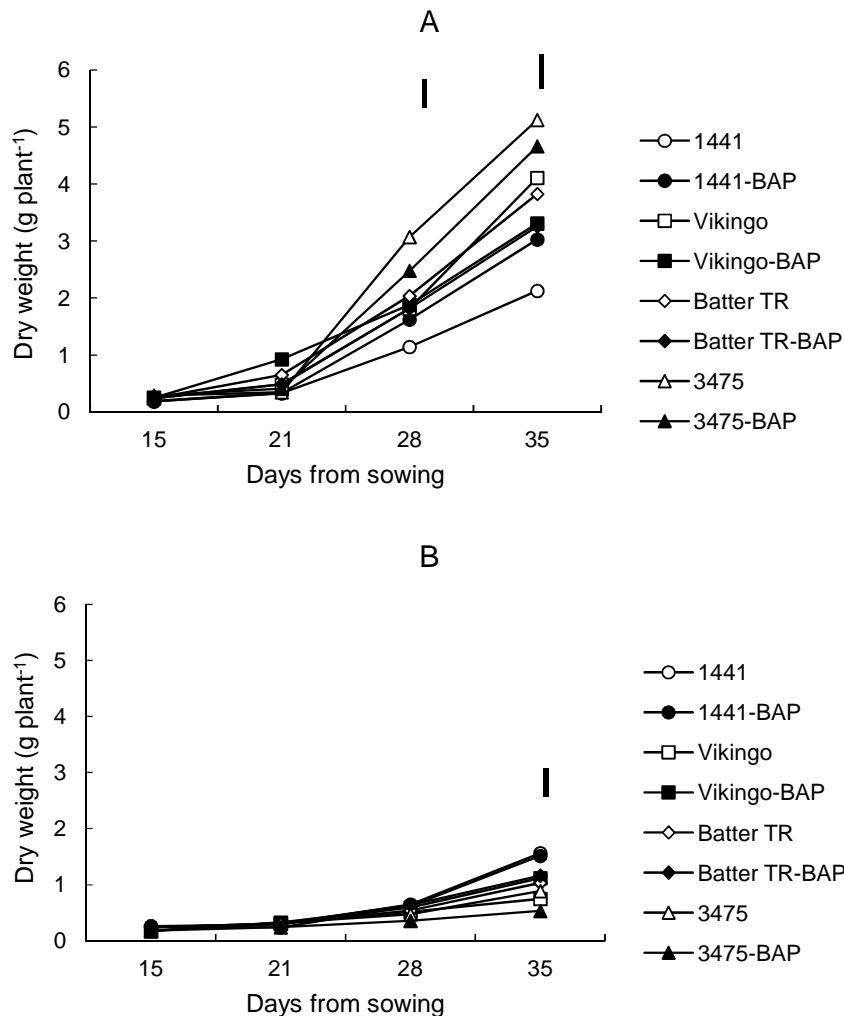

Fig. 1. Changes in total fresh weight for four super sweet maize hybrids under direct-seeded (A) or transplants (B) sprayed with zero (control plants, empty symbols) or 50 mg l⁻¹ BAP (full symbols). Vertical lines indicate least significant differences (LSD) (n = 10)

Table 1. Changes in the rate of leaf appearance (RLA), the relative leaf area expansion rate (RLAE) and the specific leaf area (SLA) for four super sweet maize under transplant or direct-seeded and sprayed with zero (control plants) or 50 mg l⁻¹ BAP. Different lowercase letters indicate significant differences (P < 0.05) between control and BAP-sprayed plants, while different capital letters indicate significant differences (P < 0.05) among sowing routines for each sweet maize hybrid tested (n = 10)

	RLA (leaves week^{-1})	RLAE (cm^{2}cm^{-2} day^{-1})	SLA (cm^2 g^{-1})
'1441'			
Direct-seeded			
Control	0.182^{bA}	0.124^{bA}	45.35^{bA}
BAP	0.202^{aA}	0.139^{aA}	55.95^{aA}
Transplant			
Control	0.138^{bB}	0.096^{aB}	43.93^{aA}
BAP	0.166^{aA}	0.106^{aB}	39.39^{aA}
'3475'			
Direct-seeded			
Control	0.178^{aA}	0.140^{aA}	40.22^{aA}
BAP	0.174^{aA}	0.130^{aA}	38.68^{aA}
Transplant			
Control	0.117^{bB}	0.056^{aB}	44.48^{aA}
BAP	0.139^{aB}	0.070^{aB}	31.67^{bA}
'Vikingo'			
Direct-seeded			
Control	0.173^{aA}	0.132^{aA}	40.63^{bA}
BAP	0.163^{aA}	0.121^{aA}	49.71^{aA}
Transplant			
Control	0.114^{bB}	0.063^{aB}	40.17^{aA}
BAP	0.152^{aA}	0.070^{aB}	39.16^{aA}
'Butter TR'			
Direct-seeded			
Control	0.173^{bA}	0.136^{aA}	40.22^{aA}
BAP	0.202^{aA}	0.129^{aA}	38.68^{aA}
Transplant			
Control	0.152^{bB}	0.078^{aB}	44.48^{aA}
BAP	0.178^{aB}	0.087^{aB}	31.67^{bA}

Positive relationships between RLAE (r^2 = 0.813 P < 0.001) (Fig. 2A), RGR (r^2 = 0.780 P < 0.001) (Fig. 2B) and NAR (r^2 = 0.805 P < 0.001) (Fig. 2C) and root DW were found. The higher values were those from control plants.

3.2 Field Experiments

Significant higher seedling emergence in transplant were found with the higher differences in 'Vikingo' super sweet maize hybrid (Fig. 3).

Low plant density (4 plants m^{-2}) give higher RLAE and NAR in all super sweet maize hybrids; direct-seeded plants showed higher values than transplanted ones. On the other hand, the higher CGR values were found when the higher plant density was used (8 plants m^{-2}). Only minor differences related to a single BAP spray were found in RLAE and NAR but control showed higher CGR values than BAP-sprayed plants. (Table 4).

Super sweet maize hybrids tested showed the higher LAI and RUE when cropping at 8 plants m^{-2}. Direct-seeded plants developed a canopy with higher LAI than transplanted ones, with slight effects related to a BAP spray. Sowing routines had minor effects on RUE. The highest differences in HI was found between sowing routines; transplanted plants showed higher values than direct-seeded ones. Only minor differences of a single BAP spray on HI was found (Table 5).

Table 2. Changes in the relative growth rate (RGR), the net assimilation rate (NAR) and the leaf area ratio (LAR) for four sweet maize mutants under transplant or direct-seeded sprayed with zero (control plants) or 50 mg l^{-1} BAP. Different lower case letters indicate significant differences (P < 0.05) between control and BAP-sprayed plants, while different capital letters indicate significant differences (P < 0.05) among sowing routines for each sweet maize hybrid tested (n = 10)

|	RGR (g g^{-1} day^{-1})	NAR (g cm^{-2} day^{-1}) (x 10^{-5})	LAR (cm^2 g^{-1})
'1441'			
Direct-seeded			
Control	0.154[bA]	7.67[aA]	200.80[aA]
BAP	0.132[aA]	6.83[aA]	193.08[aA]
Transplant			
Control	0.100[aB]	5.47[aB]	183.59[aB]
BAP	0.096[aB]	4.92[aB]	194.63[aA]
'3475'			
Direct-seeded			
Control	0.146[aA]	7.40[aA]	196.68[aA]
BAP	0.136[aA]	6.86[aA]	197.75[aA]
Transplant			
Control	0.071[aB]	4.24[aB]	168.38[bB]
BAP	0.054[bB]	2.79[aB]	192.06[aA]
'Vikingo'			
Direct-seeded			
Control	0.130[aA]	7.23[aA]	179.41[aA]
BAP	0.114[bA]	6.54[aA]	173.76[aA]
Transplant			
Control	0.048[aB]	3.08[aB]	156.23[aB]
BAP	0.048[aB]	2.99[aB]	160.81[aA]
'Butter TR'			
Direct-seeded			
Control	0.129[aA]	6.74[aA]	190.55[aA]
BAP	0.123[aA]	6.37[aA]	192.77[aA]
Transplant			
Control	0.067[aB]	3.58[aB]	186.74[aA]
BAP	0.072[aB]	3.99[aB]	180.26[aA]

C
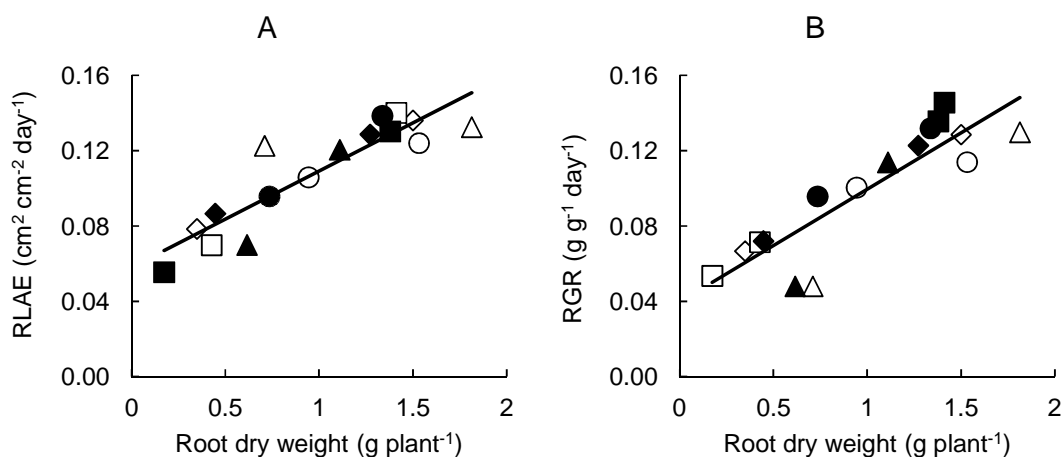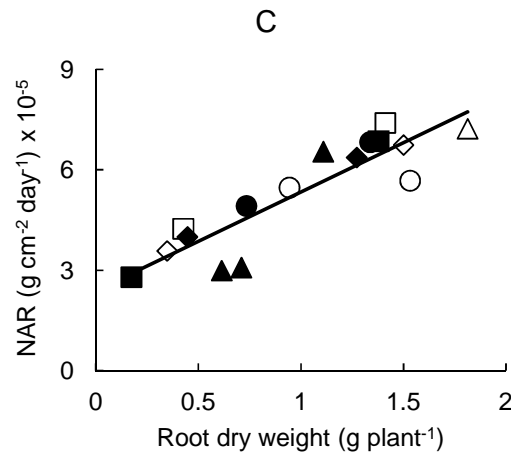
Fig. 2. Relationship between RLAE (A), RGR (B) and NAR (C) in plants of four sweet maize mutants under transplant or direct-seeded sprayed with zero (control plants, empty symbols) or 50 mg l^{-1} BAP (full symbols)

The straight-line regressions were RLAE = 0.051 root DW + 0.058 (r^2 = 0.813 P < 0.001), RGR = 0.060 root DW + 0.040 (r^2 = 0.780 P < 0.001), NAR = 2.94 root DW + 2.40 (r^2 = 0.805 P < 0.001) (n = 10). '1441': ○-●, 'Vikingo': Δ-▲; 'Batter TR': ◊-♦, '3475': □-■
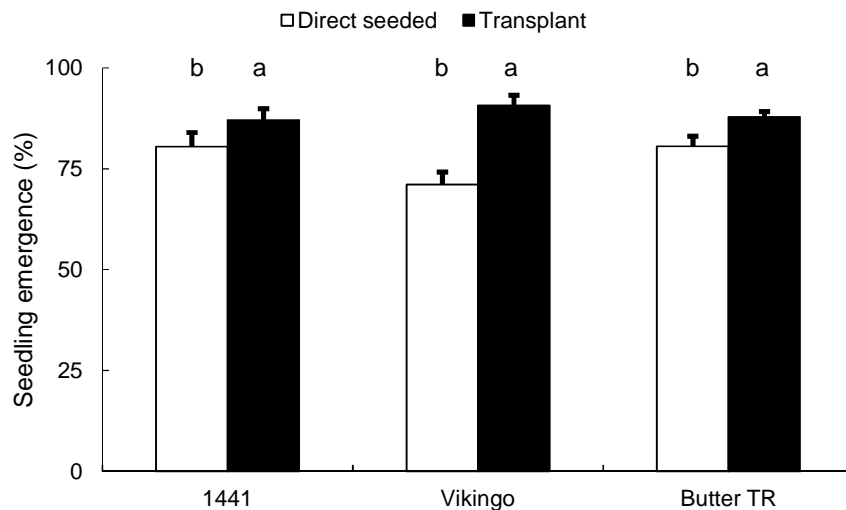

Fig. 3. Seedling emergence (%) for three super sweet maize hybrids under direct-seeded or transplant. Standard errors are indicated. Lower-case letters indicate statistically significant differences (P < 0.05) between direct-seeded and transplanted plants for each super sweet maize hybrid (n = 6)

Earl yield per plant was higher in crops grown at the lower plant density (4 plants m^{-2}). At low plant density, control direct-seeded plants showed higher yield than transplanted ones, but there is no significant yield differences when crops grown at 8 plants m^{-2}. A single BAP spray increased yield in transplants to the values found in control plants. On the other hand, when yield was indicated on a field soil base (hectare), the higher values were found at 8 plants m^{-2} plant density and in the transplanted crops (Table 6).

Positive relationships between RLAE (r^2 = 0.639 P < 0.001) (Fig. 2A), CGR (r^2 = 0.754 P < 0.001) (Fig. 2B) and plant yield (r^2 = 0.726 P < 0.001) (Fig. 2C) and root DW were found when data for

all sweet maize hybrids and treatments were plotted.

Table 3. Changes in allometric relationships between roots and shoots and between stem and leaves for four sweet maize mutants under transplant or direct-seeded sprayed with zero (control plants) or 50 mg I^{-1} BAP. The slope straight-line (β) are indicated. The probability of the slope being zero was P < 0.001. Different lower case letters indicate significant differences (P < 0.05) between control and BAP-sprayed plants, while different capital letters indicate significant differences (P < 0.05) among sowing routines for each sweet maize hybrid tested (n = 10)

	Root: shoot β	Stems: leaves β
'1441'		
Direct-seeded		
Control	0.894[aA]	0,940[aB]
BAP	0.817[bA]	0,933[aB]
Transplant		
Control	0.778[aB]	1,008[aA]
BAP	0.714[bB]	1,016[aA]
'3475'		
Direct-seeded		
Control	0.855[aA]	0.874[bB]
BAP	0.797[bA]	0.948[aB]
Transplant		
Control	0.648[aB]	0.973[aA]
BAP	0.533[bB]	0.979[aA]
'Vikingo'		
Direct-seeded		
Control	0.903[aA]	0,937[aB]
BAP	0.806[bA]	0,916[bB]
Transplant		
Control	0.764[aB]	0,919[bA]
BAP	0.777[aB]	1,022[aA]
'Butter TR'		
Direct-seeded		
Control	0.892[aA]	0,941[aB]
BAP	0.824[bA]	0,864[bB]
Transplant		
Control	0.794[aB]	0,976[aA]
BAP	0.698[bB]	0,973[aA]

4. DISCUSSION

The use of different super sweet maize hybrids, two sowing routines, two plant densities and a BAP spray (which presumably increase endogenous cytokinin content) give a range of yield in plants grown at the same PAR availability. On the other hand, this work include both plant and crop approaches which considering the influence of the edaphic environment on root growth and its correlative effects on super sweet maize yield.

The accumulation of biomass by crops results from PAR intercepted by the canopy, and from the efficiency with which the intercepted PAR is converted into dry matter [16]. In maize crops, kernel set has been associated with intercepted radiation around anthesis [14]. The expansion and duration of green leaf area determine the fraction of incident radiation intercepted by the crop [43].

The pot experiment was limited to the first growth stage; this is, from sowing and the seventh expanded leaf (V$_7$ stage). Our results showed that the accumulated fresh weight (Fig. 1) at the end of the experiment was higher in direct-seeded control plants than in transplants ones, in agreement with previous field experiments [12, 13,22]. Usually, transplants delay leaf area expansion and both fresh and dry weight accumulation as indicated by RLA (Table 1), RLAE (Table 1) and RGR (Table 2). At the same time, transplants and the BAP-sprayed plants increased photosynthetic capacity estimated through NAR (Table 2) and photo assimilate partitioning toward shoots (Table 3). But the novelty results was achieved in Fig. 2 because it showed that RLAE, RGR and NAR, as growth parameters which, can estimate leaf area expansion, biomass accumulation and photosynthetic activity respectively are positively related to root dry weight during the first stage of growth. Previous reports in pot ornamentals [28,29,30,31] are in agreement with the hypothesis that roots driven shoot biomass accumulation, at least when plants are grown under an abiotic stress such as the 'root restriction' syndrome. Bartoli et al. [44] and Zwack & Rashotte [45] have claimed that the close coordination between root and shoot growth is controlled by a signaling pathway which is largely hormonal, with a major site of control located in the root system [46]. Mi et al. [47] showed multiple signaling pathways control in maize plants as well.

Leaf area is important in determining the percentage of solar radiation intercepted by a plant and it therefore influences plant growth and final yield. Rattin et al. [22] indicate that a lower leaf area from transplants let to increase plant density because critic leaf area index, defined as the plant biomass which let intercept 95% of

radiant photosynthetic light, only is achieved during the short period of V_T (pre-anthesis phase) when a high plant density (12 plant m^{-2}) was used. Data from Tables 4 show that RLAE was higher at the lowest plant density (4 plants m^{-2}) while Table 5 indicate that the leaf area index (LAI) was higher with 8 plants m^{-2}. Anyway, direct-seeded plants ever show higher values than transplants for both growth parameters.

When pot and field experiments was matched, NAR was significant highest in field plants (Table 4) than in pot ones (Table 2) which indicate that the photosynthetic capacity per unit area of the super sweet plants was significantly higher at the end of the growing cycle. In agreement, Sánchez-Andonova et al. [13] showed that transplants retain more green leaf area than direct-seeded plants during grain filling. These leaves have the highest photosynthetic rates in the canopy and its senesce more slowly than all other leaves,

maintaining a high photosynthetic rate into the grain-filling period. On the other hand, data from Table 5 show that RUE was higher in direct seeded plants at lower plant density (4 plants m^{-2}) but an inverse result was found at the highest plant density (8 plants m^{-2}). Anyway, plant density had a higher effect on the crop growth rate (CGR) than sowing routine (Table 4).

High yields in sweet maize crops are related to high and homogeneous plant population after emergence. Although it has been indicated that the low field emergence and early field vigour in cold soils are major problems in *shrunken-2* maize hybrids [48,49,50], data from Fig. 3 showed emergence percentages higher than 70% for the three super sweet hybrids even under direct-seeding. Emergence percentages in transplants were significant higher. These data are in agreement with our previous reports [51,13,22].

Table 4. Changes in the relative leaf expansion area (RLAE), the crop growth rate (CGR), the net assimilation rate (NAR) and the leaf area ratio (LAR) for three sweet maize mutants under transplant or direct seeded at two plant densities (4 and 8 plants m^{-2}) and sprayed with zero (control plants) or 50 mg l^{-1} BAP. Different lowercase letters indicate significant differences (P < 0.05) between plant densities, while different capital letters indicate significant differences (P < 0.05) among sowing routines for each sweet maize hybrid tested (n = 6)

	RLAE (cm^2 cm^{-2} day^{-1})		NAR (g cm^{-2} day^{-1}) (x 10^{-5})		CGR (g m^{-2} day^{-1})	
	Plant density (plants m^{-2})		Plant density (plants m^{-2})		Plant density (plants m^{-2})	
	4	8	4	8	4	8
'1441'						
Direct-seeded						
Control	0.126^{aA}	0.054^{bA}	72.66^{aB}	60.73^{bA}	1242.49^{aB}	2981.84^{aA}
BAP	0.141^{aA}	0.056^{bA}	91.75^{aA}	50.87^{bB}	1183.58^{aB}	2212.85^{aA}
Transplant						
Control	0.109^{aB}	0.071^{bA}	86.98^{aA}	64.85^{bA}	1069.85^{bB}	2536.64^{bA}
BAP	0.095^{aB}	0.070^{bA}	86.71^{aA}	63.30^{bA}	1101.22^{aB}	1943.31^{bA}
'Vikingo'						
Direct-seeded						
Control	0.130^{aA}	0.053^{bA}	70.27^{aB}	53.17^{bB}	1292.97^{aB}	2615.96^{bA}
BAP	0.121^{aA}	0.051^{bA}	72.14^{aB}	53.81^{bB}	1312.95^{aB}	2442.97^{aA}
Transplant						
Control	0.070^{aB}	0.070^{aA}	87.68^{aA}	63.91^{bA}	1341.50^{aB}	3256.40^{aA}
BAP	0.072^{aB}	0.066^{aA}	85.02^{aA}	68.63^{bA}	1164.77^{bB}	2559.93^{bA}
'Butter TR'						
Direct-seeded						
Control	0.129^{aA}	0.050^{bA}	73.68^{aA}	54.10^{bB}	1105.20^{aB}	2402.04^{bA}
BAP	0.132^{aA}	0.047^{bB}	75.81^{aB}	60.30^{bB}	1121.99^{aB}	2466.27^{bA}
Transplant						
Control	0.088^{aB}	0.064^{bA}	80.54^{aA}	86.46^{aA}	934.26^{bB}	3432.46^{aA}
BAP	0.096^{aB}	0.074^{bA}	92.03^{aB}	78.81^{aA}	1196.39^{aB}	2845.04^{bA}

Table 5. Changes in the leaf area index (LAI), the radiation use efficiency (RUE) and the harvest index (HI) for three sweet maize mutants under transplant or direct seeded at two plant densities (4 and 8 plants m^{-2}) and sprayed with zero (control plants) or 50 mg l^{-1} BAP. Different lowercase letters indicate significant differences (P < 0.05) between plant densities, while different capital letters indicate significant differences (P < 0.05) among sowing routines for each sweet maize hybrid tested (n = 6)

| | LAI (m^2 m^{-2}) | | RUE (g MJ^{-1} m^{-2} day^{-1}) | | HI | |
| | Plant density (plants m^{-2}) | | Plant density (plants m^{-2}) | | Plant density (plants m^{-2}) | |
	4	8	4	8	4	8
'1441'						
Direct-seeded						
Control	1.71^{bA}	4.91^{aA}	0.0167^{bA}	0.0183^{aB}	0.320^{aB}	0.302^{aB}
BAP	1.29^{bA}	4.35^{aA}	0.0186^{bA}	0.0248^{aA}	0.411^{aB}	0.342^{bB}
Transplant						
Control	1.23^{bB}	3.91^{aB}	0.0106^{bB}	0.0263^{aA}	0.428^{aA}	0.392^{aA}
BAP	1.27^{bA}	3.07^{aB}	0.0090^{bB}	0.0246^{aA}	0.448^{aA}	0.420^{bA}
'Vikingo'						
Direct-seeded						
Control	1.84^{bA}	4.92^{aA}	0.0095^{bA}	0.0159^{a}A	0.335^{aB}	0.268^{aB}
BAP	1.82^{bA}	4.54^{aA}	0.0107^{bA}	0.0172^{aB}	0.450^{aA}	0.303^{bB}
Transplant						
Control	1.53^{bB}	4.00^{aB}	0.0114^{bA}	0.0167^{aA}	0.436^{aA}	0.328^{bA}
BAP	1.37^{bB}	4.75^{aA}	0.0125^{bA}	0.0233^{aA}	0.436^{aA}	0.379^{bA}
'Butter TR'						
Direct-seeded						
Control	1.50^{bA}	4.44^{aA}	0.0187^{bA}	0.0212^{aB}	0.325^{aB}	0.330^{aB}
BAP	1.48^{bA}	4.09^{aA}	0.0175^{bA}	0.0222^{aA}	0.358^{aB}	0.349^{aB}
Transplant						
Control	1.16^{bB}	3.97^{aB}	0.0102^{bB}	0.0246^{aA}	0.375^{bA}	0.424^{aA}
BAP	1.30^{bB}	3.61^{aB}	0.0085^{bB}	0.0177^{aB}	0.480^{aA}	0.430^{bA}

Although Mock and Pearce [52] suggested a LAI higher than 4 for a maize crop, only limited data for super sweet maize crops are available. Anyway, direct-seeded crops would be adjust to this suppose more than transplant ones (Table 5). The usually lowest PAR interception for sweet maize crops are even lower for transplant crops [13,22]. Ordás et al. [53] and Butrón et al. [54] indicated a clear relationship between aerial environment and sweet maize mutant hybrids. However, our data showed that RLAE (Fig. 4A), CGR (Fig. 4B) and yield (Fig. 4C) are positively related to root dry weight (the correlation coefficient r^2 are 0.639, 0.754 and 0.726 respectively). The usually super sweet maize small plants [12] increased the possibility to extract the most root system during the second experiment at field. This new approach would indicate that root growth could be considered as a limiting factor to shoot growth.

Although root system architecture is known to be highly plastic and strongly affected by environmental conditions, we have little understanding of the underlying mechanisms controlling root system development [55,56]. The physiological significance of root growth would be related with the endogenous hormonal balance because the root apical growth meristems synthesized most of the endogenous cytokinins [57,58,59]. While El-Hendawy et al. [60] found a positive relationship between a decrease in root growth and drought, Alí et al. [61] suggested that this abiotic stress can be overlapped with the same BAP dose (50 mg l^{-1}) applied in our experiments. On the other hand, O'Hare and Turnbull [62] showed that zeatin ribosides (the active form of the endogenous cytokinins) increased with an increase in root growth. Canopy structure define both photosynthetic rate and endogenous hormonal balance. Boonman and Ponds [63] and Boonman et al. [64,65] found a positive relationship between PAR radiation and endogenous cytokinin concentrations. Foliar application of 50 and 100 mg l^{-1} BAP significant increase growth

characters and photosynthetic pigments in maize blades at different stages of growth; the higher BAP concentration the higher yield and its components [66].

Table 6. Earl yield for three sweet maize mutants hybrids under transplant or direct-seeded at two plant densities (4 and 8 plants m^{-2}) and sprayed with zero (control plants) or 50 mg l^{-1} BAP. Different lowercase letters indicate significant differences (P < 0.05) between plant densities, while different capital letters indicate significant differences (P < 0.05) among sowing routines for each sweet maize hybrid tested (n = 6). Ear number in direct-seeded plants was decreased by germination-emergence losses. Mean post-transplant losses were near 2%. Yield, on an area basis (ton fresh weight ha^{-1}), was calculated as the product of ear fresh dry weight by ear number

|	Yield (g plant^{-1})		Yield (ton ha^{-1})	
	Plant density (plants m^{-2})		Plant density (plants m^{-2})	
	4	8	4	8
'1441'				
Direct-seeded				
Control	372.22^{aA}	222.39^{bA}	11.49^{bA}	14.32^{aB}
BAP	334.00^{aA}	209.97^{bA}	12.80^{bB}	13.52^{aB}
Transplant				
Control	298.92^{aB}	198.66^{bA}	11.96^{bA}	15.89^{aA}
BAP	350.56^{aA}	191.88^{bB}	14.02^{bB}	15.35^{aA}
'Vikingo'				
Direct-seeded				
Control	330.33^{aA}	200.91^{bA}	11.62^{aB}	11.42^{aB}
BAP	337.67^{aB}	202.60^{bA}	11.36^{aB}	11.52^{aB}
Transplant				
Control	306.11^{aA}	171.35^{bA}	12.64^{bA}	13.71^{aA}
BAP	329.00^{aB}	178.43^{bA}	13.16^{bA}	14.27^{aA}
'Butter TR'				
Direct-seeded				
Control	317.56^{aA}	219.02^{bA}	11.33^{bB}	14.99^{aB}
BAP	345.78^{aA}	227.66^{bA}	10.92^{bB}	15.58^{aB}
Transplant				
Control	298.83^{aB}	211.46^{bA}	11.95^{bA}	16.92^{aA}
BAP	374.17^{aA}	249.13^{bA}	14.97^{bA}	19.93^{aA}

A

B

C
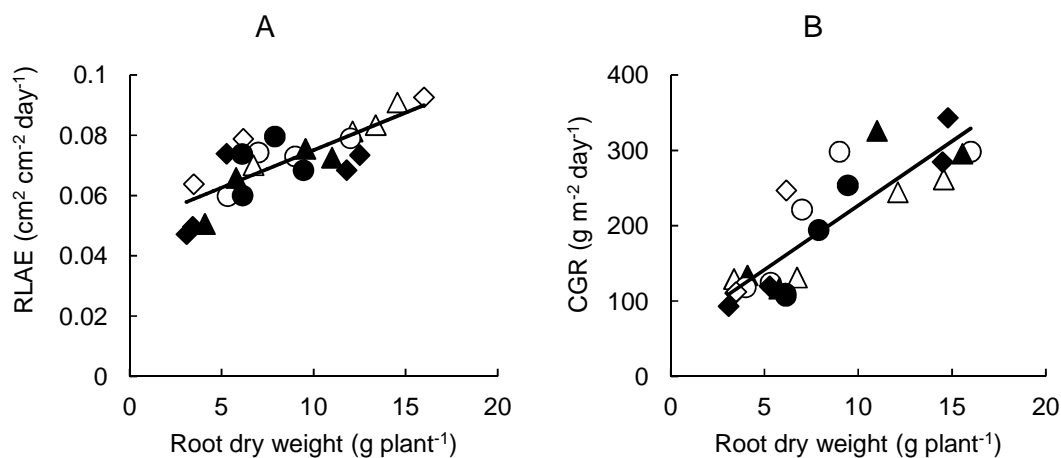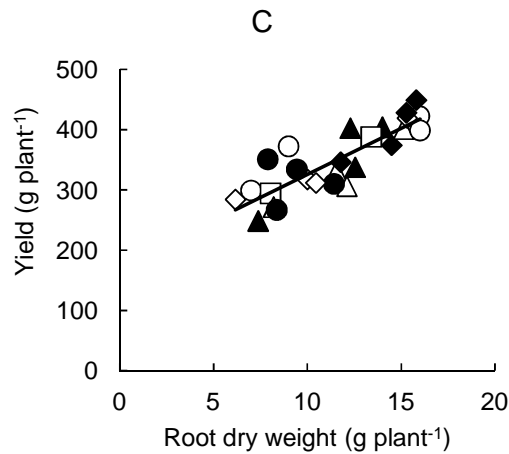
Fig. 4. Relationship between the relative leaf area expansion rate (RLAE) (A), the crop growth rate CGR (B) and yield (C) in plants of three sweet maize mutants under transplant or direct-seeded sprayed with zero (control plants, empty symbols) or 50 mg l^{-1} BAP (full symbols)
The straight-line regressions were RLAE = 0.0025 root DW + 0.050 (r^2 = 0.639 P < 0.001), CGR = 17.05 root DW + 56.34 (r^2 = 0.754 P < 0.001), Yield = 15.26 root DW +173.10 (r^2 = 0.726 P < 0.001). '1441': ○-●, 'Vikingo': Δ-▲; 'Batter TR': ◊-♦

Yield of an individual plant has been usually related with the shoot growth rate between emergence and harvest, as the result of the PAR irradiance and light interception by the crop [14,67]. However, we found no significant yield differences between plants direct-seeded or transplants at commercial plant density (8 plants m[-2]) (Table 6) [13,22]. Changes in photo assimilate allocation would explain the lack of yield differences between plants direct-seeded and transplanted, which showed different total leaf area expanded, RLAE (Table 4), LAI and RUE (Table 5). The higher HI in transplants and in all BAP-sprayed plants and the plant allometries root: shoot and stem: leaves (Table 3) are in agreement with this hypothesis. The higher photo assimilate fluxes during the grain-filling period reinforce ear activity as the main plant sink [68]. On the other hand, the finding of Gordon et al. [69] explain how increasing cytokinin concentration leads to the first steps in reestablishing the shoot stem cell niche. At the same time, Francis and Halford [70] suggested that tissues and organs with high endogenous cytokinins such as the shoot apical meristem are sinks of photo assimilates.

Super sweet yield (ton ha^{-1}) are the product of the ear fresh weight (at R_3 stage), the ear number (only one in the modern *sh2* hybrids cropping at high densities) and the plant number per unit soil area. Our results showed that transplants give higher ear yield on a soil area base than direct-seeded crops because the higher final plant number per unit area. A BAP spray and transplant optimize yield at low plant density (4 plants m[-2]) but did not change yield at higher plant density (8 plants m[-2]). These results are in agreement with our previous reports [13,22]. Liu et al. [71] have indicated that non-uniform plant spacing within the row in corn may reduce grain yield and explain our results at low plant densities.

According to Cramer et al. [72] who indicate that natural environment of plants offer a set of biotic and abiotic stresses and determine correlative complex responses, our results showed that roots partially drive super sweet maize hybrids yield, presumably through changes in endogenous cytokinins synthesis such as has been previously hypothesized.

5. CONCLUSIONS

Data showed that super sweet maize yield are the result of PAR and ground stimulus, which determine both photo assimilate production and partition. The use of a transplant routine let higher plant densities and better light interception, especially during grain filling. On the other hand, transplants reinforce ear activity as the main plant sink; the result is a higher super sweet maize yield per unit soil area. Added exogenous cytokinins as a single BAP spray, increase yield. A combined transplant routine

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and a single BAP spray give come of the highest super sweet yields.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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