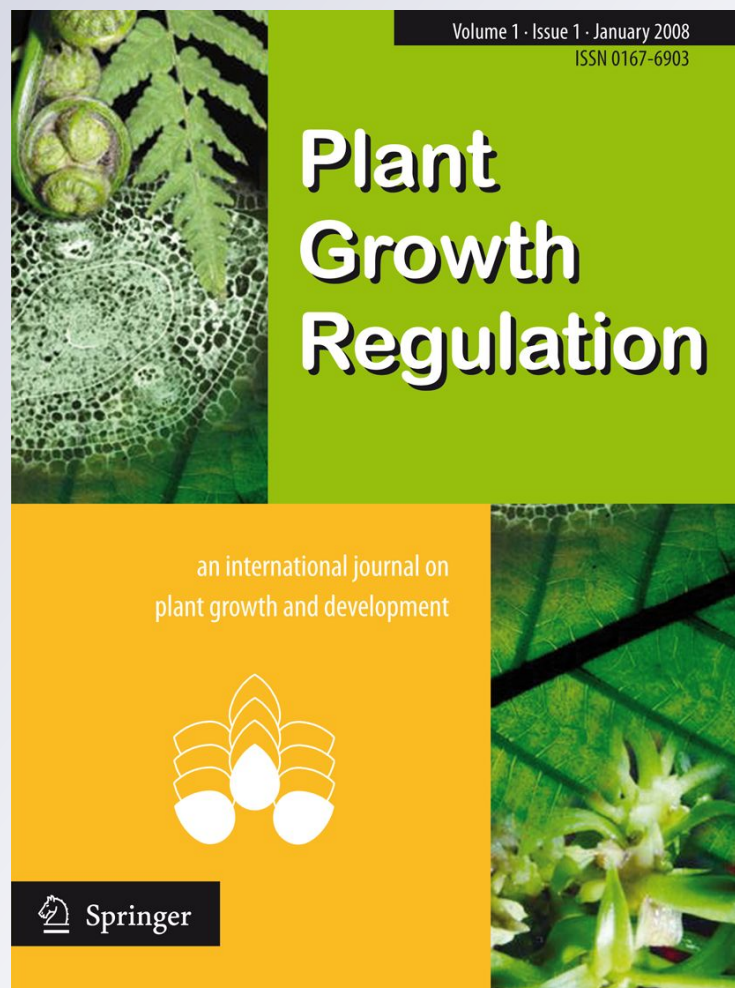# ABA action on the production and redistribution of field-grown maize carbohydrates in semiarid regions

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# ABA action on the production and redistribution of field-grown maize carbohydrates in semiarid regions

**Claudia Travaglia · Guillermo Balboa · Gabriel Espósito · Herminda Reinoso**

**Abstract** The aim of this study is to analyze the response of exogenous abscisic acid (ABA) application in plants grown under field conditions in semiarid zones in order to increase maize production. For this, it is necessary to understand the factors, such as the size and capacity of transport system involved in the mobilization and distribution of assimilates. The vascular transport capacity of ABA-treated and control plants was compared in terms of number of vascular bundles, phloem area per bundle, and the proportion of phloem in the ear peduncle of female inflorescences. This study showed that the application of exogenous ABA in field-grown maize under moderate drought allows a greater amount of maize production, an increase in the level of photosynthetic pigments, the carbohydrates remobilization to grain, and the capacity of this transport by an increase in the number of vascular bundles and the phloem area in peduncle. Evidence obtained in this study suggests that ABA could help improve agricultural production in rain-fed crops in which irrigation is not possible. This will allow us to follow a new technological strategy to increase the effective filling of organs during crops in unfavorable water conditions.

**Keywords** Abscisic acid (ABA) · Maize · Carbohydrates · Phloem · Yield · Water stress

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## Introduction

Maize (*Zea mays* L.) is severely affected by drought when it occurs close to flowering, as it inhibits floral development and leads to zygote abortion and fertilization failure (Otegui et al. 1995; Saini and Westgate 2000). In this stage, grain yield is reduced more than in other stages of growth due to the fact that flowering is a critical period in the determination of the number of kernels which is, in turn, the main yield component (Andrade et al. 1999; Çakir 2004).

The deficiency in the translocation of photoassimilates to the spike during this period is one of the main causes of this reduction (Schussler and Westgate 1991). It has been reported that increases in the reductive sugars (glucose–fructose) in wheat (Kameli and Lösel 1993) and maize (Pelleschi et al. 1997; Schellenbaum et al. 1998) leaves are an indicative of the water stress effect. This is why the soluble sugars have been considered markers to detect genotypes tolerant to dehydration in these crops. The reduction in the number of kernels caused by water stress can happen even when the amount of viable pollen is abundant (Moss and Downey 1971; Grant et al. 1989).

A close association has been made between the kernel abortion and the carbohydrate supply during flowering (Zinselmeier et al. 1999; McLaughlin and Boyer 2004). The photoassimilates produced during the photosynthesis in plants must be distributed from the zones of synthesis or storage (source) to all the organs that need the photoassimilates (sink) in order to satisfy the requirements of metabolism and growth. The amount of product to be transported and the distances they must travel require a specialized system of transport, which is the phloem. The transport through the phloem depends on the production of

metabolites in the sources, on the concentration gradient of the solutes along the transport route, and phloem unloading in the sinks. The transport is potentially limited by any of the processes cited (Guardiola and García-Luis 1993; Thorpe et al. 1997). Therefore, the transport is strongly influenced by the phloem loading at the sources, and it is the sink that controls its direction. However, the transport capacity of the phloem and the anatomic characteristics of the phloem tissue ensemble can be a limiting factor in the mobilization of assimilates between the source and the sink.

The generation of alternative strategies for the improvement of farming crop productivity and yield such as maize, under limiting edaphic conditions such as water deficit, represents an important research field to provide technological variants to the farming sector. In this sense, the use of phyto-regulators could be considered useful in order to enhance the plant water balance, growth, and productivity. It is well known that the endogen concentration of abscisic acid (ABA) is changed according to environmental changes, mainly due to an increase in stress situations (Bray 1991). Furthermore, it has been widely proven that ABA decreases water loss by regulating stomatal closure (Little and Eidt 1968; Mittelheuser and van Steveninck 1969; Jones and Mansfield 1970; Raschke 1987). ABA is also related to the promotion of dry matter accumulation in storing organs (Wang et al. 1998) or to growth increase when ABA action avoids the temporal water stress (Sansberro et al. 2004; Travaglia et al. 2009). Our previous findings indicate that ABA treatments increase yield under moderate drought in field-grown wheat (kg/ha), when ABA application enhances the transport of photoassimilates from the leaves and the stem to the developing grains, without modifying quality (Travaglia et al. 2007, 2010), in agreement with the results found in rice (Yang et al. 2003).

Although the roles of ABA in basic physiology have been extensively studied, little is known about the effects of ABA applied to field-grown crops. Therefore, the aim of this study is to analyze the response of exogenous ABA application in maize plants grown under field conditions in semiarid zones in order to increase maize production, after relieving the detrimental effect of water stress, and enhance the availability of carbohydrates.

For this, it is necessary to understand the magnitude and distribution of the phloem in relation to the total cross-area of the peduncles of female inflorescences in ABA-treated and control plants. Our hypothesis is that the greater the availability of carbohydrates, the greater the phloem area in treated plants. This will allow us to follow a new technological strategy to increase the effective filling of organs during crops in unfavorable water conditions.

## Materials and methods

### Site description

The experiments were conducted in a field at the University of Río Cuarto, Córdoba, Argentina (33°07′S, 64°14′W). The soils of this region correspond to the Hapludol type: thick texture, minimal organic matter, and edaphic water, factors that limit the potential for high grain yield. The moisture retention curves of Hapludol soils are characterized by an abrupt change in the slope at ca. 0.3–0.4 MPa, in which small decreases in water content cause important increases in water retention. This is a characteristic of these types of soil texture (Kraus et al. 1996).

### Climatic conditions

Water deficit was estimated when the soil water content fell below 50%; such a situation was reached at R1 and R3 in the 2008/2009 experiment, with water content at field capacity of 47 and 46%, respectively, using Ritchie and Hanway's (1982) scale. High temperatures and the lack of humidity in the profile affected the crop development during the critical stage of flowering and kernels filling, while in the 2009/2010 experiment, humidity was greater due to higher crop water supply, both edaphically and atmospherically (records kept by the Meteorological Station, UNRC).

### Experimental procedure

The experiments were conducted in the experimental field during the spring–summer seasons of 2008/2009 and 2009/2010. Treatments consisted of foliar sprays of the entire plant with water (control) or a 300 ppm solution of ABA (±-S-*cis*, *trans* ABA, 90%, Kelinon Agrochemical Co., Beijing, China), which amounted 1 mM and 100 l per hectare at 15 days pre-anthesis (V13). Both solutions included 0.1% ethanol (a minimum amount to dissolve the ABA) and 0.1% of Triton X, and spraying was done at dawn to prevent ABA photo-destruction. The ABA dose was chosen after preliminary experiments, which was tested in a range from 150 to 350 ppm (Travaglia et al. 2007), and according to the experience with other species (Sansberro et al. 2004). In the dose chosen (300 ppm), solutions were effective spraying about 7.5 mg of phytohormone per m$^2$. The experiment consisted of a randomized block design, with six replicates for each treatment, and a plot was sown with 10 rows and 5 m long. The maize variety used was Dekalb DK 747 MG RR, the most widely used by farmers according to recommendations for this region.

Measurements

The variables analyzed in this study took into account the photoassimilates production and partitioning toward the corncob and the yield components.

At harvest, the yield components were all measured: ear length and diameter, row number, number, and average weight of grains per ears. To determine total grain yield, all kernels were removed and weighed from all ears in 1 m$^2$ per plot for each treatment.

For pigment measurement, 50 mg fresh weight of the leaf was homogenized in a mortar with 10 ml of 80% acetone. The homogenate was loaded into Eppendorf tubes, and after 1 h at 4°C to allow pigment extraction, it was centrifuged twice at 5,000 rpm for 5 min. Aliquots were taken, and chlorophylls *a* and *b* levels were measured by spectrophotometry at 650 and 665 nm, respectively. Five milliliter of 1 M NaOH and 15 ml of diethyl ether were added to the total volume. Carotene content was assessed from the ether fraction by spectrophotometry at 450 nm (modified from Mackinney 1938). Samples were obtained at R1, R3, and R5.

Total water-soluble carbohydrate determination was based on the phenol–sulfuric acid method. Six samples were processed for each treatment, and 100 mg of shoot was homogenized in a mortar with 1.5 ml of 1% TCA. The homogenate was loaded in Eppendorf tubes and centrifuged twice for 10 min at 7,500 rpm. Aliquots of 20 µl were taken and added to 500 µl of phenol reactive (phenol 0.5% in water), followed by 2.5 ml of sulfuric acid. A serial dilution of glucose from 0 to 100 mg ml$^{-1}$ was used to determine the calibration curve. After 10 min at room temperature, the mixture was recorded by spectrophotometry at 488 nm, and the results of the samples were compared with those of the glucose calibration curve (modified from Daniels et al. 1994). Samples were obtained at R3 and R5.

The percentage of carbon remobilization (% CR) was estimated according to Yang et al. (2000), where % CR = [(NSCsa − NSCsm)/(NSCsa) × 100], NSCsa = nonstructural soluble carbohydrates in shoots at anthesis, and NSCsm = non-structural soluble carbohydrates in shoots at maturity. Samples were obtained at R1 and R6.

Cross-sections of the peduncles of the upper female inflorescences were collected for the anatomic analysis. Samples were obtained at R3. The sections of the peduncles were processed using microtechnical methods, following the Johansen's recommendations (1940), which involved the use of tissues in dehydration, infiltration and paraffin embedding, rotary microtome cutting, staining, and observation. A standard Zeiss Model 16 microscope was used to assess the histological preparations, and photomicrographs were taken with a Zeiss Axiophot microscope with an AxioVision 4.3 image capture and digitalization piece of equipment and an AxioCam HRc camera.

The area covered by the peduncles was estimated from the prints on photographic paper by dividing the cross-section of the peduncle in quadrants within which two regions were delimited: the peripheral (approximately a fifth of the length of the radius from the epidermis) and the internal region. In this way, each peduncle was divided into eight zones, which were cut out and measured with an Iproplus area integrator. Later, the units that resulted from the integrator were converted, obtaining the area of each of the eight zones of each peduncle. In each quadrant and in each region of the quadrant (peripheral and internal), vascular bundles of peduncles were counted and classified into three relative sizes: small, medium, and large. Later, the area covered by the phloem in each of the bundle sizes was estimated.

The results were analyzed for variance using the Info-Stat statistical analysis software (professional version 1.1) and the LSD Fisher, and a 5% test was used to compare differences among treatments.

## Results and discussion

The results obtained in the experiment conducted in the 2009/2010 spring–summer had similar results to those found in the 2008/2009 experience, but the ABA action did not show marked differences from the control one. This fact could be due to climatic variations year by year, since the water deficit was higher in the first experience than in the second one. Following this and the results of similar experiences with other species such as wheat and soybean since 2003 in the field at different water regimes (Travaglia et al. 2007, 2009, 2010), we have proved that the ABA action benefit is only obtained when water stress is moderate. The results are described below.

Yield and some yield components

The ABA treatment increased all yield components analyzed, rising significantly the yield per hectare (more than 15%) in comparison with the control treatment (Table 1).

When water-deficit stress occurs during the critical developmental stages (anthesis, silking, rain-fill), the grain yield and kernel weight are reduced (Robins and Domingo 1953; Claassen and Shaw 1970; Grant et al. 1989). The presence of corncob without grain in the end was observed in both the treated and control plants, due to high temperatures with relatively low humidity in the environment that affected pollination and fruit set. The ABA applications seemed to have reduced sterility problems, showing less yield loss under rain-fed crops (Table 1). The kernel

size is affected by environmental stress (Aldrich et al. 1986), and a decrease in the number of kernel rows is said to diminish the vigor and size of the plant (Emerson and Smith 1950). Yields increase of ABA-treated plants is mainly due to a bigger number of kernels, coincident with a greater ear diameter and length (Table 1). This can be attributed to the fact that the applications of this phytohormone were made at the moment of the corncob formation and the number of ovules. On the other hand, the grain weight increased (Table 1), providing evidence that ABA would favor the transport and partitioning of photoassimilates for the grains filling.

### Photosynthetic pigments

The photosynthetic pigment content, chlorophylls *a*, *b* and carotenoids, was higher in leaves of ABA-treated plants in different phenologic stages (Table 2; Fig. 1).

A more prolonged photosynthetic activity favors a greater accumulation of dry material in products to harvest (Thomas and Howarth 2000). In this respect, we observed that the leaves of maize plants remained green longer in ABA-treated plants when compared to control plants (data not shown).

Although the chlorophyll *a* contents have always exceeded those of chlorophyll *b* (Table 2), since in high plants the pigment is more abundant (Gross 1991), its relationship in the R5 stage increased in the ABA-treated plants and decreased in the control plants. Therefore, these plants early showed some foliar senescence signs (Wolf 1956) in comparison with the ABA-treated plants previous to physiological maturity. This could extend the photosynthetic apparatus stability and allow a greater photosynthetic activity as time goes by, what means a greater dry matter accumulation in the harvest of grains (Thomas and Howarth 2000; Radford 1967).

Our previous results (Travaglia et al. 2007) and the findings reported in this study indicate that ABA application increases both chlorophylls in plants grown under water stress, thereby delaying leaf senescence.

Carotene contents increased in the ABA-treated plants (Table 2). Carotenoids could be a contributory factor in maintaining the integrity of the photosynthetic apparatus, especially the chloroplast, as they have indirectly reduced the formation of reactive oxygen species (ROS) (Foyer and Harbinson 1994). However, there are numerous reports that
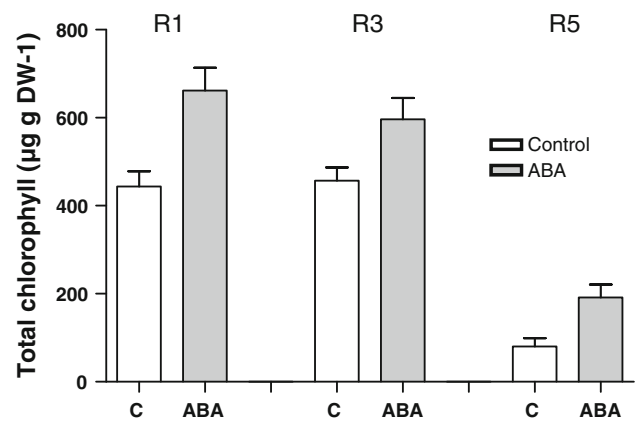
**Table 1** Yield and some yield components of maize plants treated or not with ABA at harvest

| Harvest | Control | ABA |
|---|---|---|
| n° Grains/row ear | 31 a | 34 b |
| n° Rows/ear | 14 a | 16 b |
| Length ear (cm) | 14.87 a | 15.69 b |
| Diameter ear (cm) | 15.08 a | 15.64 b |
| n° Grains/plant | 460 a | 520 b |
| Weight grains/plant (g) | 114.23 a | 132.41 b |
| Yield (kg ha$^{-1}$) | 4,569 a | 5,312 b |

Different letters mean significant differences from control at $P \leq 0.05$ for the Fisher test



**Fig. 1** Total chlorophyll content (µg g DW$^{-1}$) in control leaves and ABA-treated plants at the R1, R3, and R5 phenological stages. *Bars* show SE of 12 replicas

**Table 2** Photosynthetic pigment quantification

| Stage | Leaf tissue | Chl *a* | % of C | Chl *b* | % of C | Carrot | % of C |
|---|---|---|---|---|---|---|---|
| R1 | Control | 363.03 a | 42.18 | 80.63 a | 80.29 | 0.43 a | 55.81 |
| | ABA | 516.15 b | | 145.37 b | | 0.67 b | |
| R3 | Control | 383.54 a | 24.36 | 73.65 a | 61.86 | 0.49 a | 26.53 |
| | ABA | 476.96 b | | 119.21 b | | 0.62 b | |
| R5 | Control | 64.62 a | 147.54 | 16.04 a | 98.57 | 0.14 a | 107.14 |
| | ABA | 159.96 b | | 31.85 b | | 0.29 b | |

Chlorophylls *a*, *b* and carotene content in control and ABA-treated plants at different phenological stages, expressed as µg/g fresh weight and percentage of control (% of C). Data represent the means from 12 samples, and the different letters mean significant differences from control at $P \leq 0.05$ for the Fisher test

state that ABA applications inhibit the photosynthetic process (Reddy et al. 2004; Liu et al. 2005), although Ivanov et al. (1995) have reported that ABA applied to barley seedlings increased the total carotene concentration and had a protective effect on the photosystem II (PSII) complex, making plants avoid the harmful effect of high-intensity light. The latter is known to play an important role in maintaining the integrity of the photosynthetic membranes under oxidative stress (Munné-Bosch and Alegre 2002).

Production and remobilization of carbohydrates reserves from leaf and stems to the grains

Abscisic acid (ABA) application increased carbohydrates availability in shoots at R3 stage (25 days after application), in comparison with control plants (Table 3a). This is beneficial when considering the close association of the increase in grain abortion when the provision of carbohydrates decreases during flowering (Zinselmeier et al. 1999; McLaughlin and Boyer 2004). Furthermore, there are many reports (Suzuki 1989; Al Hakimi et al. 1995; Kerepesi et al. 1998; Slafer et al. 2003) that show a positive relationship between the content of sugars and the degree of tolerance to abiotic stress in cereals, suggesting that the more sugar content, the more tolerance in plants.

On the other hand, ABA-treated plants showed increased mobilization of the total soluble carbohydrates reserves from the leaf and stems to the grains, in comparison with the control plants (Table 3b). Maize plants are sensitive to water deficit during their reproductive period (Robins and Domingo 1953; Claassen and Shaw 1970), which can be seen in a reduction in the number of grains per unit of surface area (Kiniry and Ritchie 1985; Grant et al. 1989), due to the effect of a deficiency in the translocation of photoassimilates of the

**Table 3** (a) Average values of carbohydrates content (mg/g DW) in control and ABA-treated plants at the R3 and R5 phenological stages, and (b) difference between the average remobilization of total stem water-soluble carbohydrates in control and ABA-treated plants

| Treatments | Stage | |
|---|---|---|
| | R3 | R5 |
| **(a) Carbohydrates content** | | |
| Control | 611.09 a | 276.45 a |
| ABA | 819.35 b | 254.60 a |
| Treatments | | % Removvilization |
| **(b) Remobilization of carbohydrates** | | |
| Control | | 54.8 a |
| ABA | | 68.9 b |

Different letters mean significant differences from control at $P \leq 0.05$ for the Fisher test

spike during this period (Schussler and Westgate 1991). In agreement with these results, it has been informed that ABA application in post-anthesis in rice and wheat plants grown in pots and subjected to moderate water stress during grain filling can increase the remobilization of carbon from the photosynthetic tissues assets to grains, accelerating its filling rate (Yang et al. 2001a, b, 2004a, b).

The ABA treatment not only increased the availability of photoassimilates but also improved its transport and location in the storing organs under rain-fed crops. Thus, as suggested in a previous study (Travaglia et al. 2007), ABA could be regarded as an essential regulator in the translocation and partitioning of photoassimilates for grain filling in cereals. To better understand the relationship between the mobilizations of assimilates in maize, it is necessary to know the amount of phloem and the anatomic characteristics of the sieve tubes and companion cells.

Anatomic analysis

The monocotyledon angiosperm stems showed great diversity and complexity in relation to the course of vascular bundles (Hayward 1953). All the sections at the peduncle level showed common characteristics. In both treatments, it was found that, on average, the peripheral region of the peduncles of the female inflorescences had more small vascular bundles while the opposite was seen in the internal region. The parenchyma cells in the center were big and thin-walled, while the cells adjacent to the epidermis were smaller and thick-walled forming a protective ring inside the epidermis (Fig. 2).

The total number of vascular bundles in the peduncles of the female inflorescences was different between both treatments. On average, the ABA-treated plants showed 24 and 13% more vascular bundles than the control ones in the peripheral and internal regions, respectively. The control treatment lacked big vascular bundles in the peripheral, which were present in the ABA treatment. Besides, this treatment exceeded the number of big vascular bundles in the internal region in comparison with the control one (Fig. 2). However, the phloem area tended to be equal in the small and medium vascular bundles in both regions in both ABA-treated and control plants (Table 4).

In the ABA-treated plants, the considerable contribution to the total phloem area was remarkable, being almost 45% more than in the control treatment. In the ABA-treated plants, the phloem area per bundle, in the large bundles, tended to increase in comparison with the control treatment (Table 4). It is necessary to point out the superiority of the ABA-treated plants in the total area of phloem per vascular bundle compared with the control ones, mainly due to the presence of large vascular bundles in the internal and peripheral regions. Regarding the phloem area in individual
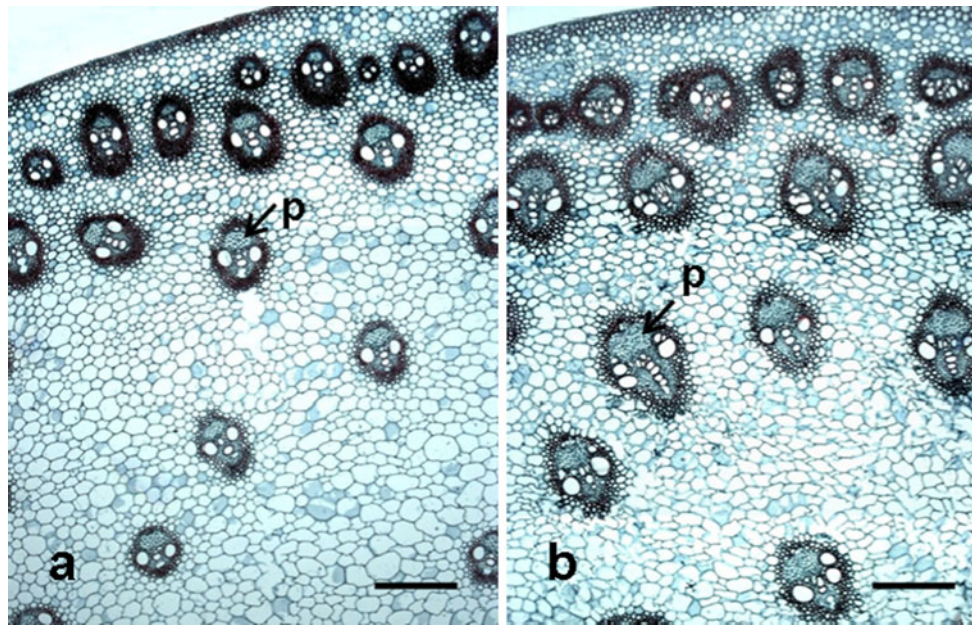
**Fig. 2** Cross-sections of the peduncles of the upper female inflorescences, in control **a** and ABA-treated **b** plants, at the R3 phenological stages, *p* phloem. *Scale bar* 400 μm

**Table 4** Average phloem area (μm$^2$) per vascular bundle in cross-sections of maize ears

| Treatments | Region | In vascular bundle | | |
|---|---|---|---|---|
| | | Small | Medium | Large |
| Control | Peripheral | 1,261.79 | 4,227.17 | 0 |
| | Internal | 2,461.43 | 5,166.36 | 8,355.88 |
| ABA | Peripheral | 1,302.98 | 4,339.85 | 9,726.90* |
| | Internal | 1,948.78 | 5,089.28 | 10,925.91* |

Asterisks mean significant differences from control at $P \leq 0.05$ for the Fisher a test

vascular bundles, the magnitude (μm$^2$) of the phloem area per vascular bundle, which globally considers the different types of cells that constitute it, corresponded closely to the size of the vascular bundles in both treatments (Table 4). When comparing regions, the peripheral bundles had less phloem area than the internal bundles. It was found that the ABA-treated plants showed a greater amount of phloem area in the vascular bundles in comparison with control plants, particularly in large bundles, both in the peripheral and internal regions. Based on the number of vascular bundles and their corresponding phloem areas, it can be stated that this ABA-treated maize has a greater structural capacity for the conduction of assimilates directly to the ears, assuming that there is a direct relationship between the phloem area and the number of sieve tubes, as stated by Canny (1975). This author, Nobel (1991), and Salvador et al. (1994) emphasized the importance of determining the actual proportion of sieve tubes for quantitative studies.

They add that although measurement is arduous and delicate, it is useful in the study of assimilate translocation since plant physiologists need to estimate transport by mass flow through these phloem cells.

ABA promoted not only phloem but also xylem enhancement. In Fig. 2, more metaxylem elements are present in the ABA-treated plants. The addition of more xylem elements improved the overall efficiency of transport of water and mineral in the entire plant. Altering the xylem vessel anatomy may influence hydraulic conductance. Working with ABA-deficient mutant plants showed that although there were more vessels in each vascular bundle, the average xylem vessel diameter was smaller than in wild-type plants (Rancic et al. 2007). This is consistent with the results of this study in which those plants without exogenous ABA had less developed xylem elements.

The spraying with ABA done at the critical time may stimulate the proliferation of procambial tissues at the peduncle of the ear to generate more vascular tissues later on; because after fertilization, the peduncle of the inflorescence continues to grow to accompany the development of the ear. However, the role of ABA in modifying vascular tissues development in response to deficit irrigation is currently under investigation.

Even when the total number of vascular bundles in both treatments was not remarkably different, the ABA treatments could indicate a greater capacity for the transport of assimilates toward the corncob, due to a bigger number of vascular bundles and a phloem area significantly superior in comparison with the control treatment. In agreement

with these results, it has been informed that the application of ABA in post-anthesis in rice and wheat plants grown in pots and subjected to moderate water stress during grain filling can increase the remobilization of carbon from the photosynthetic tissues assets to grains, accelerating its filling rate (Yang et al. 2001a, b, 2004a, b). Thus, as suggested in our previous study (Travaglia et al. 2007), ABA could be regarded as an essential regulator in the translocation and partitioning of photoassimilates for grain filling in cereals.

In conclusion, this study showed that exogenous ABA applied to field-grown maize under moderate drought allows a greater amount of maize production, an increase in the level of photosynthetic pigments, the carbohydrates remobilization to the grain, and a better capacity of this transport by an increase in the number of vascular bundles and the phloem area. The key contribution of this work is that ABA stimulates procambium proliferation, which is a novel observation.

Evidence obtained in this study suggests that ABA could help improve agricultural production in rain-fed crops in which irrigation is not possible. Although the costs of ABA applications in agriculture may not be economically feasible now, the present results open a possible future venue as long as commercial product may be available on the market. Its application will not pose any environmental threat since ABA is a natural compound produced by plants, fungi, and bacteria.

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