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ABA Increased Soybean Yield by Enhancing Production of Carbohydrates and Their Allocation in Seed

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1. Introduction

Soybean is the most expanding crop worldwide, and in the last 30 years it has doubled the cultivated area (FAO, 2002). Argentina is one of the main producers, where soybean production increased from 11 millions of tons in the campaign 1990-1991 to 55 millions of tons in the campaign 2009- 2010, with a planted area that reached 18.7 million hectares (GEA, 2010). Soybean expansion in Argentina has been so significant that the crop is now located in areas that were previously considered “marginal” or “not suitable for the crop” due to environmental conditions (Qaim & Traxler, 2005; Monti, 2008; Zak et al., 2008). In the last five years, this crop has moved approximately 4.6 millions of hectares of other crops and pasture lands (Pengue, 2009). The same as in other countries in Latin America such as Brazil, Bolivia and Paraguay, soybean culture has been the main cause of deforestation during the last years (Kaimowitz & Smith 2001; Steininger et al., 2001; Pengue, 2009).

Several technological advances have allowed the development of a new agricultural model that having less input is able to increase yields therefore generating an intensive system that in turn increases the financial profit (Monti, 2008). The use of practices such as direct sowing, fertilization, and genetically modified materials resistant to glyphosate that allow easy weed control and with high yield potential, have permitted yield increases and consolidated the new agricultural model. This agricultural model, based in monoculture, has made soybean production very economic to crop growers allowing an interesting income in a short period with low investment of resources. Argentina’s economy is greatly dependent on the currency generated by exportation of primary products and it is one of the top three producers and exporters of vegetable oils, and the biggest worldwide exporter of soybean oil (FAO, 2008). Due to the country’s size and geographical diversity, soybean has a high potential to satisfy the increasing international demand of bio-fuels (Tomei & Upham, 2009). Therefore it is possible to think in a future of increasing soybean production.

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However, although this leguminous is rich in proteins and oils, its monoculture presents risks from the point of view of the system's sustainability on the long term because of the probable negative environmental impact (Steward, 2007; Gudynas, 2008; Holland et al., 2008; Aizen et al., 2009; Altieri, 2009; Pengue, 2009). Especially regarding the organic matter soil content (the main indicator used to assess its quality and agronomical sustainability in the long term; Reeves, 1997), since in the agricultural nucleus area for the soybean crop the organic matter has been reduced from 4-5 % (original soil) to 2.5% (Cordone et al., 2005). Moreover this reduction has also impaired the soil nutrient content, the porous structure, and the soil biological activity. Nowadays, it is necessary to manage the soil appropriately in order to maintain a high grain production along the time. A system based in soybean monoculture will provoke great soil damage due to the low contribution of rubbish by the crop; in this scenario nitrogen is quickly decomposed remaining a scarce portion for the production of humus, thus leaving the soil without protection (Franzluebbers et al., 1995; Wright & Hons, 2005). This agro-ecological imbalance leads towards loss of the soils productive capacity.

A good alternative to soybean monoculture is rotation with cereals that contribute with a big mass of stubble. In the Argentinean Pampas the rotation of soybean is being performed mainly with wheat since the cycles of both crops are adapted for a continuous sequence (Andrade & Calviño, 2004). This agricultural practice however has high yield potential only in conditions of enough water availability given that the relatively high transpiratory demand of the two cultures. Also the sequence wheat/soybean/maize is used, which involves the sowing of the two gramineous in two consecutive years with the participation of soybean as the intermediate crop. This alternative provides a bigger contribution of stubbles, not only in the surface, but also in the soil volume because the mass of roots. In experiments done in soils degraded by agriculture, it has been observed that when soybean was seeded in sequences that included gramineous, yield increases by 10% as compared with those of soybean-soybean (Bacigaluppo et al., 2009).

The productive capacity of soils submitted to continuous agriculture will not be maintained by direct sowing and nitrogen fertilization since both do not provide enough carbon to repair the natural losses. Only the combination of all of these practices, i.e. direct sowing, nitrogen fertilization and rotation with cereals, will make possible to maintain the soil content of organic matter and thus to benefit the soil water balance through the presence of the harvest's rubbish on the surface that improve the soil capacity to store water (Cordone et al., 2005).

2. Yield components

In any productive system the main objective is to increase the performance; that is to say, to maximize the production of seeds by surface unit according to the availability of light, water and nutrients on each portion of land. Although the yield of soybean crops is the result of processes and changes that occur in the plants from the moment of the sowing to the harvest, it results from two main components, the number of seeds established by unit area and the seed weight (Kantolic et al., 2003). Albeit there are compensations between these two components, there is certain independence between them, which allows thinking that an increase in any of them can produce an increase in the yield (Kantolic et al., 2003). The number of seeds is the most difficult component to estimate since it depends on different factors. In soybean the flowers are arranged in open bunches that develop on the nodes. The

number of pods per node will depend on the number of fecundated flowers that last in the plant until the fruit matures, which in turn will depend on the number of nodes the plant develop, not only on its main stem but also in the lateral branches that may also vary in quantity. The mature pods can present two or three seeds, but the number of them is a character genetically stable and it does not affect the crop yield (Herbert & Litchfield, 1982; Liu et al., 2006).

Nevertheless, there is a period where the number of legumes and seeds are determined, which begins around flowering and extends through pod set, including the beginning of the seed-filling period (R1-R6). This period is called "critical period" since crop yield is established at this time (Egli, 1998). A close relationship has been found between the number of seeds per area unit and the plant growth rate during a critical period, especially between R3-R6, independently of the changes in growth for rest of the plant cycle (Jiang & Egli, 1995; Board & Tan, 1995). During the critical period both the production of reproductive organs and its survival are defined.

The final weight of the seed depends on the growth rate and the duration of grain filling, and both factors are genetically determined and vary according to the environmental conditions. The duration of the reproductive period can be changed by manipulating the plant responses to the environmental factors that control its development, particularly temperature and photoperiod; these factors act simultaneously in the plants and there are evidences of their interaction (Sinclair et al., 1991; Kantolic et al., 2003). Though temperature has influence during the whole crop cycle, the photoperiod starts its regulation when the juvenile part ends. The main effect of the photoperiod is induction of flowering; the soybean is a short day plant because the beginning of the process of flowering is induced under days getting shorter (Hicks, 1978). The photoperiod influences and regulates the major part of the reproductive events by conditioning the beginning and the ending of the different phases and the rate of these changes inside the plant (Kantolic et al., 2003). Since a long time ago many authors demonstrated the existence of a genetic variability in the sensibility of the soybean crop to the photoperiod during the period of post-flowering (Thomas & Raper, 1976; Guamet & Nakayama, 1984; Ellis et al., 2000; Kantolic & Slafer, 2001). Recently, it has been established for soybean cultivars of indeterminate growth that an increase in the photoperiod length could extend the time of the critical period and so the time that determines the seeds; such response was observed in a wide range of photoperiods longer to those required for each cultivar studied (Kantolic & Slafer, 2005).

To increase the length of the critic period through the modification of the plant responsiveness to the photoperiod would be a useful strategy to achieve a balance between photoassimilates production and sink demand. Thus, the number of legumes per node at harvest is the result of the equilibrium between production and mortality of flowers and legumes. The production of pods in turn includes the appearance of floral buds and their development in matured flowers, but then the abortion of young and matured flowers and pods are sensible to changes in photoassimilates production (Jiang & Egli, 1993; Bruening & Egli, 2000). The extension of the critical period may also have a negative effect on seeds production if during this period light or temperatures are reduced. The best diurnal temperatures for photosynthesis in soybean range between 30° and 35° C, and a decrease in pods set have been noticed below 22° C, indicating that pods number is sensible to low temperatures (Thomas & Raper, 1976; Hume & Jackson, 1981). Also, the seed growth is generally limited by the supply of assimilates, which is reduced by low temperatures (Egli, 1999). Studies under controlled conditions demonstrated that the exposition to long

photoperiods caused reduction in seeds growth rate, thus affecting negatively the seeds weight (Raper & Thomas, 1978; Morandi et al., 1988). Nowadays, several scientific and technological efforts are oriented to obtain cultivars sensible to photoperiod that by flowering earlier will further develop under light and temperature appropriate to achieve a good yield (Kantolic & Slafer, 2001). In other words, to achieve optimal environmental conditions during the critical period can be a good strategy to improve the performance due to the critical role that they have on the control of the plant development.

The weather conditions also define when and how long the yield components are determined and how much of the production arrives at end of the crop (Kantolic et al., 2003). However, water deficiencies or any stress that affects the photoassimilates production and transport during the critical period reduces the number of pods per node and the number of seeds at harvest. During dry farming, and even under irrigation, plants may suffer daily variations of water supply (an unbalance between what roots absorbed and leaves transpired) that generate stressful situations. If such stress is mitigated during the crop's critical period, its performance may be improved. This objective becomes really important when soybean varieties of short cycle are used, since they have a shorter critical period than those of long cycle. In fact, the major part of soybean in South America is cultivate in rain fed, and variability in crops performance is strongly related with differences in rain's total amount and distribution along the plant's cycle and soil water availability. Since water availability is an important limitation for the application of the strategy before mentioned, the success of any crop not only depends on water supply but also on the plant's ability to use it (Andriani, 1997). Thus, crops with long cycle cultivars are more flexible and balanced than those with short cycle cultivars, like those used to rotate with wheat. The later have a high yield potential when there is good water availability, particularly during the period where the number of seeds is defined. Therefore, a way of improving the performance of short cycle soybean crops is to optimize water usage. To achieve this will let to obtain a more profitable soybean harvest, and to maintain an appropriate rotation of the crops. Such benefit could be achieved through induction of partial stomata closure in a way that the concentration of intracellular CO₂ would be enough for photosynthesis, and at the same time water losses may be minimized (Kang et al., 1998).

3. Absciscic acid functions

The phytohormone abscisic acid (ABA) regulates a variety of physiological plant processes, including seed maturation, seed and bud dormancy, root growth, foliar senescence and the transition between the vegetative to reproductive development, among others (Leung & Giraudat, 1998).

When plants are confronted to abiotic stresses, ABA is the main candidate in the plant's responses signaling, since it is well known that the phytohormone concentration varies according to the stressful situation (Zhu, 2002). In fact, ABA acts as signal in the plant responses to environmental stresses imposed by either cold, drought and/or high levels of salt, through the modulation of genes sensible to stress (Christmann et al., 2006). It has been proven that during periods of stress synthesis and concentration of ABA may drastically vary in specific tissues (Zeevaart & Creelman, 1988). For example, under conditions of water stress the concentration of ABA in leaves can increase up to 50 times in a period of 4 to 8 hours; after rehydration ABA levels are reduced to normal in a similar period of time (Taiz & Zeiger, 2006). This relationship strongly suggests that ABA is one of the mediators of the

plant responses to the stressful conditions (Galau et al., 1986; Zeevaart & Creelman, 1988; Bray, 1991; Christmann et al., 2006; Hirayama & Shinozaki, 2007).

It has been demonstrated that ABA is able to alleviate the water stress not only in daily variations but also in long term draught by provoking a stomatal closure, since stomata are responsible for the major proportion of plant water losses (Leung & Giraudat, 1998; Zhang & Outlaw, 2001; Taiz & Zeiger, 2006). In fact, the signal transduction in guard cells in response to ABA has been well documented (Luan 2002; Levchenko et al., 2005; Pei & Kuchitsu 2005; Vahisalu et al., 2008).

During seed development, ABA has a main role in regulating synthesis of proteins and lipids and in promoting the seed's tolerance to dryness. This hormone has also a protective role for the seed by inducing embryonic dormancy not allowing its early germination and inhibiting it in conditions of osmotic stress. As well, ABA has been identified as one of the main chemical signal that regulates genetic expression during stress (Seo & Koshiba 2002). Different evidences suggest that the hormone perception may be produced both extra and intracellular (Bray, 1997; Finkelstein et al., 2002). Although it has not been identified yet a primary receptor of the hormone, there are a wide variety of second messengers involved that contribute to the signaling pathway (Moreno, 2009). In different species, the application of this hormone increased the plant resistance by provoking the expression of ABA-dependent genes.

For the expression of specific genes in response to water and saline stresses, the existence of two types of signal chains have been postulated, one that depends on ABA and another independent of the hormone (Chandler & Robertson, 1994; Shinozaki & Yamaguchi-Shinozaki, 1997). Within the ABA-dependent signal chain there is production of proteins with protective function, enzymes responsible for osmolite synthesis, antioxidant enzymes, transcription factors and other proteins involved in the responses to water stress (Bray, 1997; Xiong et al., 2002). Amongst the main proteins are the dehydrins, which are highly hydrophilic and replace water in its function of maintaining the structure of other proteins and membrane phospholipids protecting the cell cytoplasm of dehydration (Hare et al., 1999). There are also the LEA (late embryogenesis abundant proteins) proteins, that form many families of proteins accumulating at high levels during the matured period of embryogenesis, just before the moment of the seed drying (Moreno, 2009). Some of them are accumulated in vegetative tissues in response to the osmotic stress generated by different factors such as dehydration, salinity, cold and freezing (Baker et al., 1988; Bray, 1993). The information available about different LEA proteins indicates that they have an important role in the protection against the cell's dehydration (Battaglia et al., 2008).

As well, the synthesis of osmoregulators like proline, glycine-betaine, sugars and sugar alcohols are related with the cells osmotic status since these components facilitate the water uptake by the plant (Cushman, 2001). Over-expression of some of the genes that lead the synthesis of osmoregulators have been used to protect plants to the osmotic stress in many species (Abebe et al., 2003; Tamura et al., 2003; Waditee et al., 2005; Hmida-Sayari et al., 2005; Ashraf & Foolad, 2007). On the other hand, antioxidant enzymes together with non protein components protect plants from free radicals that are generated due to an increase in the rate of O₂ photoreduction in chloroplasts (Danon et al., 2004; Robinson & Bunce, 2000). Among the main antioxidant enzymes are superoxide dismutase, catalase, ascorbate peroxidase, peroxidase, glutathione reductase and monodehydroascorbate reductase (Apel & Hirt, 2004).

During the water stress the expression of different transcription factors that mediate the gene response to the stress is also induced; some of these transcription factors are related to specific sequences in the region that promotes the genes (Guiltinan et al., 1990; Busk et al., 1997).

ABA is also able to activate metabolization of carbohydrates temporally stored in the stem of rice (Yang et al., 2003) and wheat (Travaglia et al., 2007 and 2010) plants. As well, ABA applications lead to the accumulation of carbohydrates in grains consequently accelerating the filling process. The application of fluridone, inhibitor of carotenes and (hence) ABA synthesis, leads to reduction in the activity of enzymes related with starch synthesis (Grappin et al., 2000).

4. ABA promotes yield in field-cultured soybean

The roles of ABA in basic physiology have been extensively studied, but information regarding participation of this hormone in field crops eco-physiology is rather limited. The evaluation of stress effects under artificially controlled conditions is very useful to recognize the physiological plant response and allows determining the presence of mechanisms of resistance. Such mechanisms could be useful traits of cultivar selection in programs of genetic performance. However, the plant responses under these conditions may not be representative of what happens in field conditions. Growth and development of a crop under field conditions is the product of the interaction among a series of genetic and environmental factors, so the formulation and application of agronomic practices for the crop's improvement will depend on the understanding of the eco-physiological basis for their development.

Taking into account all the antecedents cited, we worked with the following hypothesis: "a plant that grows in a field and receive the stress signal (i.e., it is treated with ABA) before a situation of stress is produced, it is then more prepared to face the stress and the effect is minimized".

From here on we inform the results obtained by our research group in evaluating the effects of ABA applications on the performance of a short cycle cultivar (GM 3.4, Dekalb, Argentina) of *Glycine max* L. under field conditions. The experiments were performed during three consecutive years through direct sowing in rain fed conditions at the experimental field of the Universidad Nacional de Río Cuarto Campus, Río Cuarto, Provincia de Córdoba, Argentina (33° 07' S, 64° 14' W). Sowing density was 32 seeds m², and at harvest there were 23 plants m². The crops had a water supply during the crop seasons of 611, 466 and 571 mm of rainfall that satisfied the calculated crop's evapo-transpiration demand. The results of the field experiments were also complemented with an experiment in greenhouse. ABA (Lomon Biotech, Beijing, China, 90 % purity) was sprayed in a dose of 300 mg L⁻¹ at the phenological stages V7 and R2, which are previous and close to the critical periods; the solutions contained 0.1% Triton for emulsification, and the spraying was done at sunset to avoid ABA photo-destruction. Further details of the experimental conditions can be found in Travaglia et al. (2009).

The results showed that ABA application improved physiological variables related with the photosynthetic capacity of the plants. Control and ABA-treated plants at R5 phenological stage (beginning of seed filling), did not show differences in the length of the main stalk. However, ABA-treated plants had higher shoot's dry weight than controls (Figure 1).

Bigger stem diameter (data not shown) and increase in the foliar area of the leaves 2 and 3 (counting from the apex) as compared with the control plants were observed (Figure 2).

The leaves of these plants were greener and presented a bigger proportion of chlorophyll than the control ones (Figure 3), however they did not present main differences in the levels of carotene (data not shown).

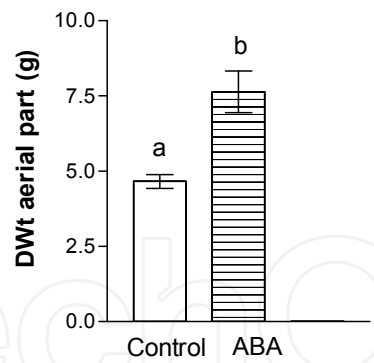


Fig. 1. Average dry weight (D Wt) in three years of experiments with field-grown soybean plants at R5. Treatments: control, ABA treated plants. Bars indicate SEM of 30 plants. Different letters show significant differences at $p<0.05$ with the Fisher alpha Test.

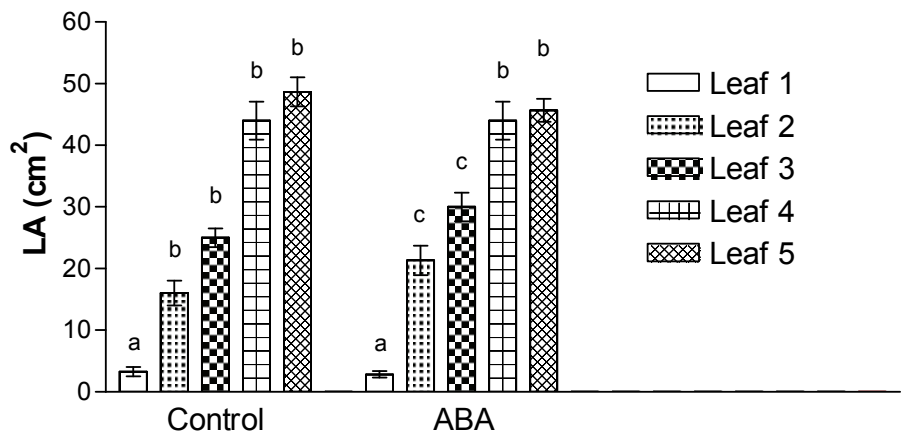


Fig. 2. Average leaf area (LA) at different plant levels in three years of experiments with field-grown soybean plants at R5. Treatments: control, ABA treated plants. Bars indicate SEM of 30 plants. Different letters show significant differences at $p<0.05$ with the Fisher alpha Test. Figure adapted from Travaglia et al. (2009).

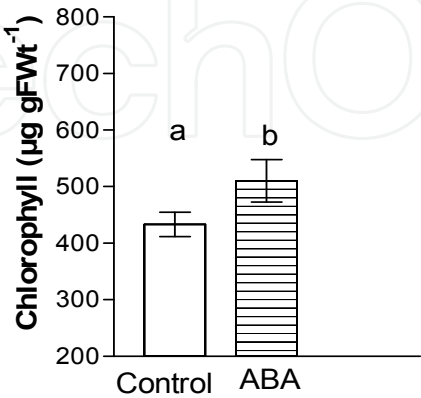


Fig. 3. Average of total chlorophyll content in three years of experiments with field-grown soybean plants at R5. Treatments: control, ABA treated plants. Bars indicate SEM of 15 plants. Different letters show significant differences at $p<0.05$ with the Fisher alpha Test.

Generally, the action of ABA has been related with processes of inhibition, although there is recent evidence of its presence in developing tissues where it may have a promoting action (Finkelstein & Rock 2002; Sansberro et al., 2004; Peng et al., 2006). Our results demonstrate that ABA sprayed to the leaves benefits dry matter accumulation favoring vegetative growth of soybean plants grown in field conditions (Travaglia et al., 2009). For the cultivar and the dose used, no restraint of shoot growth was observed as had been previously reported (Sloger & Caldwell, 1970). These results coincide with those found in field-grown wheat plants under water stress that had been treated with ABA, in which these plants showed higher shoot biomass accumulation (Travaglia et al., 2007 and 2010). This effect of ABA has also been seen in studies carried out under controlled conditions with different levels of water deficit, both in *Arabidopsis* (Finkelstein & Rock 2002) and *Ilex paraguariensis* (Sansberro et al., 2004), where the plants sprayed with ABA had greater growth than those with lower (endogenous) levels of ABA. In agreement with our previous findings (Travaglia et al., 2007 and 2010), these new results suggest that ABA is an important regulator of cell and whole-plant water content, likely due to an increased turgor that allows optimal cellular expansion (Acevedo et al., 1971).

ABA-treated soybean plants also improved leaf area, which can be considered useful since it benefits the interception of light, particularly in short cycle varieties that sometimes do not cover the soil surface until late in the cycle (Andrade & Calviño, 2004). Another interesting aspect to take into account is the photosynthetic capacity of the plant. It has been reported in literature that ABA stops the photosynthesis of different species under controlled conditions (Daie & Campbell, 1981; Xu et al., 1995; Gong et al., 1998; Wilkinson & Davies, 2002; Reddy et al., 2004; Liu et al., 2005); but our results showed an increase in the content of dry matter that increases in correlation with chlorophyll levels (Travaglia et al., 2009). These results are similar to those we observed during three years of essays with field-grown wheat treated with ABA; the treated plants showed higher levels of chlorophyll and maintained green leaves longer (5 to 10 days) than control plants (Travaglia et al., 2010). Longer photosynthetic activity should benefit higher accumulation of dry matter in harvest products (Thomas & Howarth, 2000). According to Ivanov et al. (1995) ABA had a protective effect on the photosystem II complex (PSII) in barley plants since it avoided the deleterious effect of high intensity light. ABA would act protecting the membranes, especially those of chloroplasts, when they are under stress (Travaglia, 2008). These authors also reported higher carotene levels in ABA-treated plants, an effect that was also observed in wheat (Travaglia et al., 2007 and 2010), but not in soybean. Although in this investigation the soybean plants were not under a long water deficit, they would suffer temporary water stress during hours of high light intensity where there is an unbalance between transpiration and water absorption; the ABA-treated plants showed higher chlorophyll levels and maintained green leaves longer. These results indicate that ABA protect the photosynthetic system and delayed foliar senescence under conditions of temporary water stress allowing the plant to generate and accumulate more dry matter and also produce more seeds.

The root density (number of lateral roots) was higher in ABA-treated plants as compared to controls (Figure 4). Such higher production of lateral roots is well expressed by roots dry weight improvement in ABA-treated plants as compared with controls (Figure 5). There were no significant differences in number, weight and viability of nodules in plants treated respect to the control (data not shown).



Fig. 4. Picture showing soybean plants grown in plastic pots (24 L) during 80 days; ABA-treated (left), control (right) plants. Bars = 10 cm.

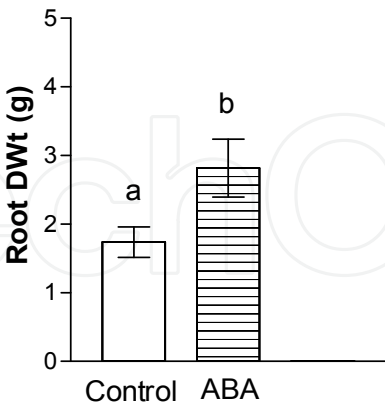


Fig. 5. Dry weight (D Wt) of roots of soybean plants grown in plastic pots (24 L) during 80 days. Treatments: control, ABA treated plants. Bars indicate SEM of 30 plants. Different letters show significant differences at $p<0.05$ with the Fisher alpha Test.

Vysotskaya et al. (2008) suggested that ABA promotes radical growth instead of any specific growth of the aerial part. Our results indicate however that ABA stimulated an increase of the total biomass. It is possible that at the beginning the application of the phytohormone

may induce the distribution of biomass towards the roots, but our results indicated an increase in the quantity of dry matter for both, aerial part and roots.

Enhancement in the number of lateral roots, therefore augmenting the density of the root system, by ABA has been previously informed for other species by Trewavas & Jones (1991). According to Lian & Harris (2005) it is an effect that ABA has on roots of leguminous species, but in non leguminous species ABA inhibits lateral root development. The increasing in the density of lateral roots provoked by ABA can be a good effect to obtain a higher number of nodules by plant.

As well, Zhang et al. (2004) found more biomass and more nodules in well-irrigated soybean plants treated with ABA or inhibitors of GA biosynthesis. In our study ABA did not affect the nodules but increased plants' root density, which is highly beneficial considering that soybean has a high requirement of N that is accumulated in seed proteins. The amount of N used for this crop is the sum of the inorganic N present in the soil and the atmospheric N that is symbiotically fixed by *Bradyrhizobium japonicum* (Madrzak et al., 1995). The crop gets ca. 50 to 60 % of its N at the beginning of the symbiosis (Salvagiotti et al., 2008). The performance of soybean is related in a positive way with the absorption of N by plant. This is supported by the findings of Salvagiotti et al. (2008), who analyzed 637 essays in USA between 1966 and 2006, observing an increase in grain yield of 13 kg per kg of N accumulated in aerial biomass. When soil aeration is minimal, such as in direct sowing, the rate of mineralization is reduced, and N immobilized and consumed by denitrifying microorganisms increases. This fact augments the necessity of N, stimulating N biological fixation (NBF) from the early stages of the crop (Bonel et al., 2005). The soybean N requirements changes according to the stage of development, increasing between R3-R6. In the Argentinean Pampas region, the contribution of NBF is ca. 40%. Any environmental situation of stress, like drought or flood, has negative repercussions in the NBF compromising yield (González, 1997). Drought also affects NBF because the nodule must have more than 80% of relative water content (RWC), otherwise the capacity of NBF is seriously reduced when RWC is below 60%. The critical period of the grain filling is compromised by any situation that affects NBF hence reducing the yield potential of the crop (Bonel et al., 2005).

As well, ABA-treated plants showed reduction in stomatal conductance during 24 h after the hormone has been applied as compared to controls, but then the conductance values kept more stable and become equal to the controls 11 days later (Figure 6). The ABA-treated plants also showed a lower foliar temperature (data not shown).

Closing of stomata immediately after ABA treatment is an expected response, but the partial (and stable) closing observed later could be accountable of regulating enough CO₂ entrance in the chlorenchyma cells to support photosynthesis and to minimize water losses, though maintaining evaporation in a way that foliar temperature is lower than in control plants. At the interface between atmosphere and plant, leaf stomata provide the entryway for CO₂ for photosynthetic carbon fixation, while preventing excessive water loss. Through their role in transpiration, stomata also help to control leaf temperature. The net stomatal conductance depends on both, plant-specific traits and signals received from the environment, which is the result of stomata functioning. It has been demonstrated that exogenous ABA promotes the closure of stomata (Zhang & Outlaw, 2001; Davies et al., 2005; Pei & Kuchitsu, 2005). So the observed low conductance immediately post-treatment was a desired answer, but the later increase of the conductance was maintained in the time. In papers related with field-grown wheat under water deficit, it is observed a similar behavior. The ABA treated plants

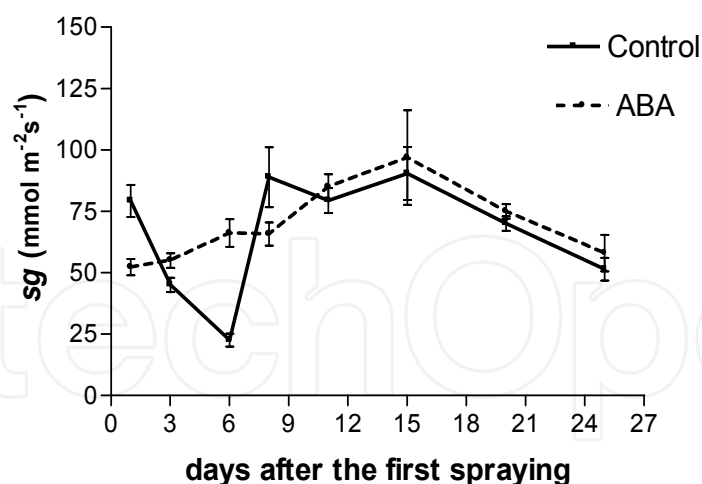


Fig. 6. Average values of leaf conductance (sg) in the 3rd fully expanded leaf (one leaf per plant, 15 plants per treatment) at 01:00 PM in three years of experiments with control and ABA-treated field-grown soybean plants since 24 h until 25 days after the first spraying. Bars indicate SEM of the 15 plants. Different letters show significant differences at $p < 0.05$ with the Fisher alpha Test. Figure taken from Travaglia et al. (2009).

closed their stomata immediately after the hormonal application, so decreasing the conductance and the rate of transpiration, but 21 days after the ABA treatment leaf conductance and transpiration rate increased more than in control plants (Travaglia et al., 2010). As well, in front of a water deficiency, the treatment with ABA had a long time effect on to the stomata behavior, maintaining some ostiolar aperture in the hours of high light while stomata in control plants are closed. This ostiolar aperture in the ABA-treated plants, although limited, was enough to maintain a leaf conductance higher than in the control plants. Although in our experiments with soybean the grade of stomata aperture was not recorded, the similarity of the results suggest that exogenous ABA promoted the immediate stomata closure, even though the plant is not under water stress, but later it benefits since stomata are maintained semi-opened with high irradiation. This may be the reason why leaf conductance is more stable along the time doing the balance between water losses and CO_2 gain more efficient. The partial stomata closure allows that the concentration of intracellular CO_2 may be sufficient so that the photosynthesis would be maximal and the water losses minimum (Kang et al., 1998). After evaluation of two leguminosae, *Phaseolus vulgaris* and *Trifolium pratense*, in front of the combined stress (drought + high temperatures), Reynolds-Henne et al. (2010) proposed that the stomata behavior is complex. However, these authors consider that in all the cases the plants achieve a balance that allows them to lose water and to avoid overheating. If stress is moderated, an important stomata closure is produced and leaf conductance is impeded giving priority to water relations, while if the stress is severe stomata conductance increases maintaining leaf temperature to avoid metabolic damages and to protect the photosynthetic apparatus. In our soybean experiments, where stress was of short time, the application of ABA immediately reduced transpiration, but in the mid term sustained water evaporation more constant so leaf temperature may be lower than in non-treated plants. Given that photosynthetic activity by crop canopy declines gradually during the effective grain filling period and current photosynthesis (rather than remobilization of stored carbohydrate) is considered to be main source for seed growth in soybean (Liu et al., 2006), supporting a regular photosynthesis could be the cause of the

higher carbohydrate amounts found at the flowering period in shoots of the ABA-treated plants as compared to controls; the difference in shoots disappears at harvest because of an increased carbohydrate remobilization (21%) to the seed in the ABA-treated plants (Travaglia et al., 2009). These results confirm the participation of ABA in promoting source to sink transport of assimilates during the stage of seed filling. This effect has been also reported in rice (Zhang et al., 1998; Yang et al., 2001; 2004), and by our group in wheat (Travaglia et al., 2007; 2010). Also in grapes, Moreno (2009) found that ABA stimulates carbon translocation from source to sink.

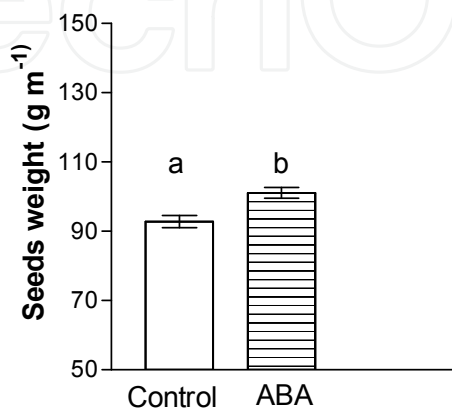


Fig. 7. Seeds weight per meter in three years of experiments with field-grown soybean plants. Treatments: control, ABA treated plants. Bars indicate SEM of 15 plants. Different letters show significant differences at $p<0.05$ with the Fisher alpha Test.

The number of ripped pods in the ABA-treated soybean plants was similar to the controls; however it was observed that during the first periods of development the pods in ABA treated plants were bigger, difference that disappeared at maturity (data not shown). The weight of seeds per m² was significantly higher in the ABA-treated plants (Figure 7); the seeds maintain the same protein content and higher oil concentration as compared with the controls (Figure 8 a and b). Thus, the treatment with ABA did not affect the quality of seeds, an important characteristic since the seed quality is one of the key aspects for agriculture success.

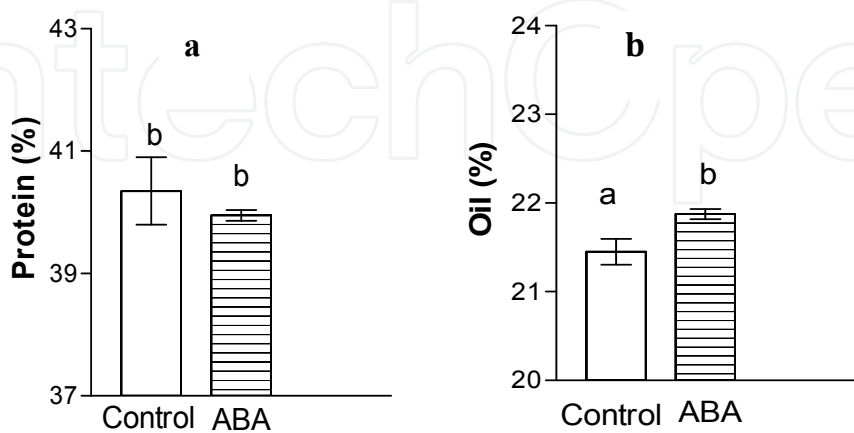


Fig. 8. Protein (a) and oil (b) percentage in grains in three years of experiments with field-grown soybean plants. Treatments: control, ABA treated plants. Bars indicate SEM of 15 plants. Different letters show significant differences at $p<0.05$ with the Fisher alpha Test.

The final chemical composition of the seeds is the result of accumulation of reserve substances in the cotyledons during the filling period. The contents of oils and proteins are influenced by genetic and environmental factors (Ojo et al., 2002; Wilson, 2004; Minuzzi et al., 2007). In the last years a better understanding of the genetic regulation in the proportions of the different components that define the quality of seeds has been achieved, and cultivars known with “enhanced value” have been obtained by traditional methods or genetic manipulation. Regarding the environment, the influence of the conditions during the seeds filling period is direct, since soybean seeds accumulate oils during this period, with a maximum rate occurring around 30 days after flowering (Wilson, 2004). The short-cycle cultivars, i.e. the short term maturity group (MG), usually have their seed filling period exposed to higher temperatures than the long-cycle MG genotypes. Yaklich and Vinyard (2004) also found higher oil concentration under high temperatures. These authors suggest that by monitoring the minimum temperatures and the daily increase during the seed filling period might have predictive value for seeds oil concentration.

It has been informed that not only the high temperatures but also the presence of water stress during the filling of seeds produces alterations in the contents of proteins and oils (Boydak et al., 2002). It is also frequently found a negative relationship between seed protein content and crop yield (Shannon et al., 1972; Yin & Vyn, 2005); moreover, there are evidences of a negative correlation between oils and proteins concentration. None of these relations were seen in our experiments since ABA enhanced both yield and seed proteins, because ABA not only increased yield but also improved the seed quality; that is, ABA did not affect protein levels but enhanced oil yield. We have also found benefits with the application of exogenous ABA in the performance of wheat grown under water restrictions. When stress was very strict, the application of ABA increased the number of grains per spike. When water stress was moderated, ABA not only increased the weight but also the number of grains. Such effect was reflected in a yield increase that ranged between 11 and 34 % (Travaglia et al., 2010). Since the food value of grain wheat relays on the protein content, it is not only necessary to achieve higher yields but also to maintain a high percentage of protein in the grain. It has been mentioned that this is difficult to achieve considering that there is an inverse relationship between yield and protein content (Cuniberti, 2001). In our study however, the grain protein content under severe drought increased in ABA-treated plants, whereas in moderate drought there was no difference in grain protein between ABA-treated and control plants (Travaglia et al., 2007 and 2010).

5. Conclusion

Recent biotechnological advances have opened great possibilities for the agricultural production and have permitted a big expansion of soybean in the Americas in general and in Argentina in particular. Having in mind that currency generation by exports is of outmost importance in the economy of the countries, everything indicates that the high production soybean system will continue.

Soybean monoculture generates a selective decreasing of the soil nutrients and can generate their exhaustion and the necessity of adding more fertilizers. According to this point of view rotation with other crops, especially cereals, seems to be an appropriate solution. However, the profits for soybean production have been differentially favorable as compared to other crops so many producers will continue with the monoculture. A profitable alternative is through practices that take into consideration the rotation of the crops; for example, short

cycle soybean-wheat. To achieve this purpose unfavorable environmental conditions during the critical period of the crops must be minimized, especially the most frequent factor that is water deficit.

The results obtained in the experiments with soybean grown in field conditions support the idea that ABA enhances yield by a combination of factors. Therefore, foliar application of ABA may be an alternative tool for enhancing yield of short-cycle soybean, since it gives relief to temporary situations of water stress, such as the stress that happens in the hours of maximum irradiance, where an imbalance between water transpiration and absorption it is frequently produced. ABA seems to improve a combination of factors that contribute to increase the number of lateral roots and the density of the radical system, to protect the photosynthetic apparatus, to keep the stomata conductance more stable over the time, and to enhance carbon allocation and partitioning to the seeds. The results presented here are also related to those obtained for wheat and other species, and open the possibility for the future use of this hormone in commercial products. Although nowadays its relative cost is high, it has decreased remarkable in the last years and some commercial products are now registered around the world; besides, its application will not represent an environmental threat since ABA is a natural compound produced by plants, fungus and bacteria.

6. References

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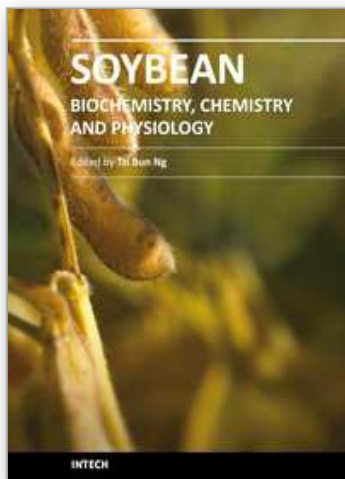
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