

International Journal of the Faculty of Agriculture and Biology,
Warsaw University of Life Sciences, Poland

REGULAR ARTICLE

Distribution of ^{14}C into biochemical components of soybean exposed to water deficit and potassium

Hedaya A. Kamel¹, Magdi T. Abdelhamid^{2*}, Mona G. Dawood²

¹ Radioisotopes Department, Atomic Energy Authority, Dokki 12311, Cairo, Egypt.

² Botany Department, National Research Centre, Dokki 12622, Cairo, Egypt.

* Corresponding author: Magdi T. Abdelhamid, E-mail: magdi.abdelhamid@yahoo.com

CITATION: Kamel, H.A., Abdelhamid, M.T., Dawood, M.G. (2010). Distribution of ^{14}C into biochemical components of soybean exposed to water deficit and potassium. *Communications in Biometry and Crop Science* 5 (1), 27–33.

Received: 15 July 2009, Accepted: 14 June 2010, Published online: 26 June 2010
© CBCS 2010

ABSTRACT

Water deficit is the primary limiting factor for successful yield of soybean (*Glycine max* L.) around the world, depending on its severity and duration, and has variable effects on several metabolic processes. Therefore, a pot experiment was conducted in a wire house at the National Research Centre, Cairo, Egypt, to examine the interactive effects of two levels of potassium fertilizer and water deficit on the distribution of ^{14}C into biochemical components (ethanol soluble compounds, oil and protein) of three Japanese soybean genotypes, non-nodulating (NN) (En 1282), nodulating (N) (Eneri) and super-nodulating (SN) (En-b0-1). The potassium (K) fertilizer levels were 25 and 150 mg K_2O kg soil^{-1} . Sixty-five days after sowing (pod filling stage), soil moisture (SM) for plants was maintained at 80% FWC for control (WW) and no water was added considered as water deficit (WD). Plant leaves were collected at 0 (at the end of exposure time), 24, 48, and 72h for measuring photosynthetic activity, total lipids and protein. The highest amount of ^{14}C was found in soluble carbohydrates after 24h in the three genotypes followed by oil and protein. K at a high level significantly increased ^{14}C fixation by 20.4 and 26.8 % in non-nodulating and normal nodulating genotypes, respectively. High K had no effect on the super-nodulating genotype. The super-nodulating genotype was characterized by lower ability for ^{14}C fixation than normally nodulating soybean at both K levels. K inhibited the detrimental effect of drought stress on photosynthesis, and this might be due to the role of K in CO_2 fixation.

Key Words: ^{14}C -distribution; potassium; soybean; super-nodulation; water deficit.

INTRODUCTION

Soybean (*Glycine max* L. Merr.) is the major world food legume. It grows in a wide range of environments under intensive and extensive management. Water deficits are a global

primary limiting factor of soybean yield, and depending on its severity and duration has a varied effect on several metabolic processes (Lawlor, 1995).

Soybean plants subjected to water stress during flower formation have shorter flowering periods (Sionit and Kramer, 1977), while water stress during later phases of soybean reproductive development has been reported to accelerate senescence, which in turn decreases the duration of seed-filling (Meckel et al., 1984).

Photoassimilate is the major substrate for plant metabolism, and most biomass yield is derived from photosynthetically-fixed carbon (C) (Jackson, 2003). Previous results with ^{14}C radioactive labeling showed that the rate and relative amount of ^{14}C photoassimilate exported out of source leaves decreased under water stress in apple (*Malus domestica* Borkh) (Li et al., 2003) but increased in *Zea mays* L. (Trouverie and Prioul, 2006). Both source and sink activities change dynamically with the development of water stress. Assimilate distribution under different fixed source activities might differ from one time to the next. Photosynthesis of source leaves returns to pre-stress levels, but the speed and degree of recovery varies with plant species and the degree of water stress (Miyashita et al., 2005).

Potassium (K) is an important plant cation involved in physiological pathways (Duke and Collins, 1985). In particular, the ability of ATPases, in membranes, to maintain active transport depends highly on an adequate K supply. Thus, efficient cell development and growth of plant tissues, translocation, assimilate storage and other internal functions, which are based on many physiological, biochemical and biophysical interactions, require adequate K in the cell sap (Marschner, 1995). Moreover, K influences plant water status and helps overcome soil moisture stress (Marschner, 1995). The impact of K was greater under low soil moisture than under optimal conditions (Sangakkara et al., 2001). However, recent studies were concerned with the distribution of photoassimilate fixed into different organs. In addition, there are no data on the effect of K on the distribution of ^{14}C fixed into biochemical components at a particular stage of water stress. This study was conducted to determine the effect of two levels of K on ^{14}C fixation by three soybean genotypes (non-nodulating, normally nodulating and super-nodulating) and its distribution in biochemical leaf components under a water deficit.

MATERIALS AND METHODS

EXPERIMENTAL PROCEDURE

A pot experiment was conducted in a wire house at the National Research Centre, Dokki, Cairo, Egypt (29.77 N, 31.3 E), from 21 May to 2 August 2007. Day temperature ranged from 28 to 45 °C with an average of 36.9 ± 3.7 °C, while night temperatures were 22.1 ± 2.8 °C with a minimum and maximum of 9 and 30 °C, respectively. Daily relative humidity averaged 40.6 ± 2.7 % and ranged between 31.1 and 46.3 %.

Soybean seeds were selected for uniformity by choosing seed of equal size and the same color. Selected seeds were washed with distilled water, sterilized with 1% sodium hypochlorite solution for about 2 minutes and thoroughly rewashed with distilled water. Five uniform air dried soybean seeds were sown along a centre row in each pot at 30 mm depth in plastic pots filled with about 7 kg soil from Giza, consisting of an upper 10 cm of soil collected from an area of undisturbed native vegetation. The soil texture was clay. To reduce compaction and improve drainage, the soil was mixed with yellow sand in the proportion of 3:1 (clay:sand) (v:v). Characteristics of the soil used in the experiment, before cultivation, were as follows. The pH was 8.52. The cations were Ca^{2+} 7.31, Mg^{2+} 3.00, Na^+ 8.26 and K^+ 1.80 meq l^{-1} , while anions were HCO_3^- 4.80, Cl^- 7.20, SO_4^{2-} 8.36 meq l^{-1} .

At sowing, granular commercial rhizobium product was incorporated into the top 30 mm of the soil in each pot with the seeds. Ten days after sowing seedlings were thinned to two per pot. Granular ammonium sulfate (20.5% N) at 40 kg N ha^{-1} and single

superphosphate (4.09 % P) at 16 kg P ha⁻¹ were added to each pot. The N and P fertilizers were mixed thoroughly into the soil of each pot immediately before sowing.

The experiment was a factorial with two levels of K fertilizer and two soil water treatments. The K and water treatments were tested on three Japanese soybean genotypes. The three Japanese soybean genotypes used in the experiment were En 1282 (non-nodulating, NN), Enrei (normally nodulating, N) and En-b0-1 (super-nodulating, SN). The two K levels were applied, i.e., 25 and 150 mg K₂O kg soil⁻¹, K1 and K2, respectively. These were equivalent to 39.5 kg (recommended dose) and 237.3 kg K ha⁻¹. The K fertilizer was mixed thoroughly into the soil of each pot immediately before sowing.

Control plants (well-watered, WW) (12 pots of each genotype, 6 pots for each K level) were watered and maintained during the whole experiment up to about 65 % FWC. From 65 days after sowing (pod filling stage), no water was added to the other 12 pots of each genotype (6 pots for each K level) which gave water deficit plants (WD).

Soil field capacity in the pots was estimated by saturating the soil in the pots with water and weighing them after they had drained for 48 h. Field capacity was 36%. The level of soil moisture was controlled by weighing pots and supplementing daily water loss twice (morning and afternoon). The soil water level treatments were maintained for 6 days from 65 to 71 days after sowing.

RADIOACTIVE COMPOUND

Radiolabeled NaH¹⁴CO₃ of original activity 23.2 MBq mg⁻¹ was purchased from Radiochemical Laboratory, Amersham, England. It was diluted with non-labeled NaHCO₃ to give a specific activity of 52.5 KBq μg⁻¹.

$^{14}\text{CO}_2$ FIXATION

At the end of day 64 (a day before water deficit application), pots were placed in a dark chamber and at the start of day 65 the pots were placed in a glass chamber where $^{14}\text{CO}_2$ was generated by the reaction between 10 % HCl and NaH¹⁴CO₃. Light was from a florescent lamp. After 15 minutes exposure, excess $^{14}\text{CO}_2$ was trapped in a 1N NaOH solution and pots were transferred to a wire house. Plant leaves were collected at time zero (the end of exposure time) and at 24, 48, and 72 h. They were frozen for 30 minutes and then oven dried and used in the following measurements.

PHOTOSYNTHETIC ACTIVITY (^{14}C -FIXATION)

To determine the amount of ^{14}C -fixed, dried tissue from the sample collected at time zero was combusted using a Harvey Biological Oxidizer (OX-600). The $^{14}\text{CO}_2$ evolved was trapped in a carbosorb scintillation cocktail and counted in a TRI-CARB 2300 Liquid Scintillation Analyzer (Packard).

LOSS OF ^{14}C FROM LEAVES

Dried samples collected at 24, 48 and 72 h after exposure to $^{14}\text{CO}_2$ were combusted and counted as mentioned above and the ^{14}C which had disappeared from the leaves calculated as follows:

$$^{14}\text{C}\text{-disappeared at a time} = ^{14}\text{C}\text{-fixed} - ^{14}\text{C}\text{-detected at that time}$$

^{14}C IN OIL

Oils were extracted in petroleum ether (60 – 80 °C) using the Soxhlet method (A.O.A.C.1990). The ^{14}C in oils was measured using a liquid scintillation analyzer.

^{14}C IN ETHANOL SOLUBLE COMPOUNDS

Oil free tissues were extracted with 80 % ethanol (v/v) (Nakayama et al., 2007). After homogenates were centrifuged using MPW-351 R Centrifuge (MPW.MED. INSTRUMENTS, Poland) with rcf 4226 for 10 min. the ethanol extract was evaporated and ^{14}C was measured using a liquid scintillation analyzer.

¹⁴C IN PROTEIN AND OTHER COMPOUNDS

Tissues remaining after extraction of oil and soluble sugars were combusted in a Harvey Biological Oxidizer (OX-600) and ¹⁴C in protein and other compounds was measured as mentioned above.

STATISTICAL ANALYSIS

The data obtained in this study were subjected to analysis of variance (ANOVA) appropriate to a randomized complete block design [(3-way for data of Table 1 (time x soil moisture x potassium) and 2-way for data of Table 2 (genotype x potassium)] after testing the homogeneity of error variances (Gomez and Gomez, 1984). The significant differences among treatments were compared with the critical difference at 5% probability by the Duncan's test.

RESULTS AND DISCUSSION

The main effects of time (24, 48 and 72 hours), soil moisture level (WW and WD) and K levels (K₁ and K₂) and their interactions on ¹⁴C-fixation (Bq g dry leaves⁻¹) of the three soybean genotypes, non-nodulating (NN), normally nodulating (N), and super-nodulating (SN) are shown on Tables 1 & 2.

The distribution of ¹⁴C to different components (ethanol soluble compounds, oil and protein) was significantly affected by soil moisture and K level in the first 72 h after initiating a water deficit (Table 1). The highest amount of ¹⁴C was in ethanol soluble fractions in the three genotypes. This was followed by oil and then protein. The ¹⁴C in ethanol soluble compounds (soluble carbohydrates, proteins, etc.) was superior in normally nodulating plants followed by non-nodulating and the least was in the super-nodulating soy beans. The non-nodulating genotype incorporated more ¹⁴C into oil more than the other two genotypes throughout the 72h. The amount of ¹⁴C in ethanol soluble compounds and oil decreased over time in the three genotypes (Table 1). However, 48 h after initiating water stress ¹⁴C lost from leaves (due to respiration and translocation to other plant parts) significantly increased with time of initiation of water deficit in all three genotypes (Table 1).

Water deficit reduced ¹⁴C in ethanol soluble compounds and protein of non-nodulating and normally nodulating plants. There was increased ¹⁴C in the biochemical components of the super-nodulating plants (Table 1). High K (K₂) significantly increased ¹⁴C in ethanol soluble compounds and protein of non-nodulating and normally nodulating plants, while there was increased ¹⁴C in ethanol soluble compounds and oil of super-nodulating plants relative to that in response to treatment K₁

Table 1 shows a significant increase in the amount of ¹⁴C lost from leaves of all three genotypes during the first 72 h after initiation of water deficit. High K (K₂) significantly decreased the amount of ¹⁴C lost from leaves of all the three genotypes compared with K₁.

The ¹⁴C that was lost from leaves may have been lost by respiration or by translocation to other plant parts such as pods, stem or roots. Since, both source and sink activities dynamically change with water stress, the distribution of photoassimilate fixed under different source activities might differ from one time to another. Further, the physiological status of source leaves, such as photosynthetic rate and sucrose accumulation concentration, that can be affected by water stress (Li and Li, 2005) can have an important effect on the export rate of newly fixed C (Dai et al., 2007).

Several studies have been concerned with translocation of photoassimilate under water deficits. Liu (1997) showed that the amount of photoassimilates exported out of labeled source leaves was relatively constant at 48 h after assimilate was fixed under water stress and well water conditions. Further, Dai et al. (2007) found that ¹⁴C-photoassimilate in leaves of control plants was relatively constant at 48 h after feeding and accounted for 50–60 % of total photoassimilate.

Table 1. Interaction and main effects of time (24, 48 and 72 h), soil moisture level (WW and WD) and two potassium levels (K1 and K2) on the distribution of ¹⁴C into ethanol soluble compounds (ESC), oil, protein (Prot.), and ¹⁴C-lost (¹⁴C-L) of three soybean genotypes, non-nodulating (NN), normally nodulating (N), and super-nodulating (SN).

Treatment	Non-nodulating				Normal-nodulating				Super-nodulating			
	ESC (Bq/g dry wt)	Oil	Prot.	¹⁴ C-L (%)	ESC (Bq/g dry wt)	Oil	Prot.	¹⁴ C-L (%)	ESC (Bq/g dry wt)	Oil	Prot.	¹⁴ C-L (%)
Interactions:												
24h*WW*K1	1924e ¹	757b	9.0ef	49.7h	2837bc	235b	9.3h	67.9d	2098c	210c	13.8e	69.6c
24h*WW*K2	3405a	376d	17.1cd	41.4i	5678a	267a	26.0f	51.2f	2801a	170d	18.3d	60.1d
24h*WD*K1	1256g	917a	6.0ef	59.4f	2427b-d	270a	7.7h	71.9cd	1987d	249b	10.7e-g	71.4c
24h*WD*K2	3054b	755b	8.0ef	41.1i	3225b	56i	14.0g	62.7e	2243b	317a	10.7e-g	65.7cd
48h*WW*K1	1573f	384d	18.0c	63.3e	1645c-e	169e	67.0b	80.4b	1209f	138e	67.0b	81.5b
48h*WW*K2	2452c	304ef	52.0a	56.7g	3055b	217c	88.0a	72.5c	1104g	240b	53.0c	81.4b
48h*WD*K1	1088h	397d	33.0b	71.7d	1355d-f	264a	37.0e	82.8b	1375e	179d	95.0a	79.2b
48h*WD*K2	2195d	330e	34.3b	60.2f	2245b-d	76h	60.0c	80.5b	2127c	181d	68.0b	68.3c
72h*WW*K1	62ij	453c	12.0c-e	88.8c	122fg	82h	10.3h	97.8a	65h	83f	8.3fg	98.0a
72h*WW*K2	135i	300ef	10.7de	94.8b	490efg	191d	47.0d	94.0a	59h	90f	10.0e-g	97.9a
72h*WD*K1	19j	157g	3.3f	98.6a	20g	151f	3.0i	98.2a	163h	15g	11.7ef	98.3a
72h*WD*K2	57ij	277f	9.7ef	94.7b	99fg	109g	10.0h	98.2a	58h	88f	7.3g	98.1a
Time:												
24h	2410a ¹	701a	10.0b	47.9c	3542a	207a	14.2c	63.4c	2282a	237a	13.4b	66.7c
48h	1872b	354b	34.3a	63.0b	2075b	182b	63.0a	79.1b	1454b	185b	70.7a	77.6b
72h	68c	297c	8.9b	94.2a	183c	133c	17.6b	97.0a	86c	69c	9.3c	98.1a
Soil moisture:												
WW	1592a ¹	429b	19.8a	65.8b	2304a	193a	41.3a	77.3b	1223b	155b	28.4b	81.4a
WD	1278b	472a	15.7b	70.9a	1401b	154b	21.9b	82.4a	1325a	172a	33.9a	80.2a
Potassium:												
K1	987b ¹	511a	13.5b	71.9a	1401b	195a	22.4b	83.2a	1149b	146b	34.4a	83.0a
K2	1883a	390b	21.9a	64.8b	2465a	153b	40.8a	76.5b	1399a	181a	27.9b	78.6b

¹Means in the same column for each treatment with the same letter are not significantly different by Duncan's test ($P < 0.05$).

Table 2 . Potassium (K) fertilizer (K1 and K2) and three soybean genotypes (non-nodulating, normally nodulating and super-nodulating) and their interactive effects on ¹⁴C-fixation (Bq g dry leaves⁻¹) in leaves of soybean plant.

Potassium level	Genotype	Non-nodulating	Normal-nodulating	Super-nodulating	Mean
K1		5359e ¹	9613b	7636c	7536B ¹
K2		6451d	12190a	7497c	8712A
Mean		5905C ¹	10901A	7566B	

¹Means in the same column or row for each treatment have the same letter are not significantly different by Duncan's test ($P < 0.05$).

Prolonged water stress increased ¹⁴C-assimilate retention (61.6 & 72.6 % at 24 h after the initiation of water stress and at the end of the experiment) in labeled leaves. Water deficit

inhibited translocation of assimilated ^{14}C from labeled leaves to other soybean parts (Zhang et al., 2007).

At zero time ^{14}C -fixation was higher in the normally nodulating genotype followed by the super-nodulating. The lowest amount fixed was in the non-nodulating cultivar (Table 2). High K level ($237.3 \text{ kg K ha}^{-1}$) significantly increased ^{14}C fixation by 20.4 and 26.8 % in non-nodulating and normally nodulating genotypes, respectively. However, the normally nodulating genotype had the greatest ^{14}C fixation followed by the super-nodulating then non-nodulating cultivars. Overall the mean of the three genotypes with K2 significantly increased ^{14}C fixation by 15.6 % compared with K1 (Table 2).

It appears that the super-nodulating genotype En-b0-1 is characterized by a lower ability to fix ^{14}C than the normally nodulating genotype at the two K levels. Takahashi et al. (2005) found that under normal conditions, the photosynthesis rate of super-nodulating Sakukei 4 tended to be higher than in cultivars Enrei and Tamahomare (normally nodulating genotypes) after the start of the seed-filling (44 days after sowing). They attributed the higher photosynthetic capability of Sakukei 4 to higher photosynthesis-related compounds in leaves, i.e., rubisco and chlorophyll (Maekawa and Kokubun, 2005). The discrepancy with our results may be due to differences in growing conditions.

Sangakkara et al. (2001) reported that K increased the photosynthetic rate in of mung bean (*Vigna radiata* L.) when grown with suboptimal soil moisture (above 50 % depletion). Kim et al. (2000) mentioned that drought stress decreased the photosynthetic rate and disrupted carbohydrate metabolism in maize (*Zea mays* L.) leaves. Both may lead to a reduced amount of assimilate available for export to sink organs and increased rate of reproductive abortion. Potassium plays an important role in translocation of photosynthates from source to sinks (Cakmak et al., 1994). Further, the K level in plant growth inhibited the detrimental effect of drought stress on photosynthesis (Berkowitz and Gibbs, 1983). This may be due to the role of K in CO_2 fixation (Marschner, 1995).

The super-nodulating genotype had a higher chlorophyll content (data not shown) than the normally nodulating plants, but its ability to fix CO_2 was lower. This may be due to some other factor than chlorophyll content, e.g., the content of enzymes involved in photosynthesis, might cause a decline in the rate of photosynthesis.

ACKNOWLEDGEMENTS

Dr. Magdi Abdelhamid is grateful to National Institute of Crop Science, Japan for providing soybean seeds to undertake this study.

REFERENCES

- Association of Official Agricultural Chemists - AOAC. (1980). *Official methods of analysis of the Association of Official Agriculture Chemists*. 12ed. AOAC, Washington.
- Berkowitz, G.A., Gibbs, M. (1983). Reduced osmotic potential effects on photosynthesis: identification of stromal acidification as a mediating factor. *Plant Physiology* 71, 905-911.
- Cakmak, I., Hengeler, C., Marschner, H. (1994). Partitioning of shoot and root dry matter and carbohydrates in bean plants suffering from phosphorus, potassium and magnesium deficiency. *Journal of Experimental Botany* 45, 1245-1250.
- Dai, Z.W., Wang, L.J., Zhao, J.Y., Fan, P.G., Li, S.H. (2007). Effect and after-effect of water stress on the distribution of newly-fixed ^{14}C -photoassimilate in micro propagated apple plants. *Environmental and Experimental Botany* 60, 484-494.
- Duke, S.H., Collins, M. (1985). Role of potassium in legume dinitrogen fixation. In: Munns, R. (Ed.). *Potassium in agriculture*. American Society of Agronomy, Madison, USA, 443-465.
- Gomez, K.A., Gomez, A.A. (1984). *Statistical procedures for agricultural research*. John Wiley, Singapore.

- Jackson, J.E. (2003). Photosynthesis, respiration and carbohydrate transport, partitioning and storage. In: Jackson, J.E. (Ed.). *Biology of apples and pears*. Cambridge University Press, Cambridge 237-267.
- Kim, J.Y., Mahé, A., Brangeon, J., Prioul, J.L. (2000). A maize vacuolar invertase IVR2 is induced by water stress. Organ/tissue specificity and diurnal modulation of expression. *Plant Physiology* 124, 71-84.
- Lawlor, D.W. (1995). The effects of water deficit on photosynthesis. In: Smirnov, N. (Ed.). *Environmental and Plant Metabolism Flexibility and Acclimation*. Bios Scientific Publishers, Oxford, 129-160.
- Li, T.H., Li, S.H. (2005). Leaf responses of micropropagated apple plants to water stress: non-structural carbohydrate composition and regulatory role of metabolic enzymes. *Tree Physiology* 25, 495-504.
- Li, T.H., Li, S.H., Wang, J., Yu, K.S. (2003). Effects of water stress at different deficit intensities on transport and distribution of ¹⁴C-assimilates in micropropagated apple plants. *European Journal of Horticultural Science* 68, 227-233.
- Liu, H.Z. (1997). *Effects of water stress on translocation and distribution of ¹⁴C-assimilates in *Amygdalus davidina* and *Malus pumila* cv. Fuji seedlings*. MSc. Thesis, China Agricultural University, China (in Chinese).
- Maekawa, T., Kokubun, M. (2005). Correlation of leaf nitrogen, chlorophyll and Rubisco contents with photosynthesis in a supernodulating soybean genotype Sakukei 4. *Plant Production Science* 8, 419-426.
- Marschner, H. (1995). *Mineral nutrition of higher plants*. Second edition. London: Academic Press.
- Meckel, L., Egli, D.B., Phillips, R.E., Radcliffe, D., Leggett, E. (1984). Effect of moisture stress on seed growth in soybeans. *Agronomy Journal* 76, 647-650.
- Miyashita, K., Tanakamaru, S., Maitani, T., Kimura, K. (2005). Recovery response of photosynthesis, transpiration, and stomatal conductance in kidney bean following drought stress. *Environmental and Experimental Botany* 53, 205-214.
- Nakayama, N., Saneoka, H., Moghaieb, R.E.A., Premachandera, G.S., Fujita, K. (2007). Response of growth, photosynthetic gas exchange, translocation of ¹³C-labelled photosynthate and N accumulation in two soybean (*Glycine max* L. Merrill) cultivars to drought stress. *International Journal of Agriculture and Biology* 9, 669-674.
- Sangakkara, U.R., Frehner, M., Nösberger, J. (2001). Influence of soil moisture and fertilizer potassium on the vegetative growth of mungbean (*Vigna radiata* L. Wilczek) and cowpea (*Vigna unguiculata* L. Walp). *Journal of Agronomy and Crop Science* 186, 73-81.
- Sionit, N., Kramer, P.J. (1977). Effect of water stress during different stages of growth of soybean. *Agronomy Journal* 69, 274-278.
- Takahashi, M., Nakayama, N., Arihara, J. (2005). Plant nitrogen levels and photosynthesis in the supernodulating soybean (*Glycine max* L. Merr.) cultivar 'Sakukei 4'. *Plant Production Science* 8, 412-418.
- Trouverie, J., Prioul, J.L. (2006). Increasing leaf export and grain import capacities in maize plants under water stress. *Functional Plant Biology* 33, 209-218.
- Zhang, M., Duan, L., Tian, X., He, Z., Li, J., Wang, B., Li, Z. (2007). Uniconazole-induced tolerance of soybean to water deficit stress in relation to changes in photosynthesis, hormones and antioxidant system. *Journal of Plant Physiology* 164, 709-717.