

BIOCHEMICAL AND PHYSIOLOGICAL CHARACTERIZATION OF OIL PALM INTERSPECIFIC HYBRIDS (*Elaeis oleifera* x *Elaeis guineensis*) GROWN IN HYDROPONICS

Caracterización ecofisiológica y bioquímica de híbridos interespecíficos de palma de aceite (*Elaeis oleifera* x *Elaeis guineensis*) crecidos en medio hidropónico

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ABSTRACT

The interspecific hybrid, *Elaeis oleifera* x *Elaeis guineensis* (OxG) is an alternative for improving the competitiveness and sustainability of the Latin American oil palm agro-industry, because of its partial resistance to some lethal diseases and also because of the high quality of its oil. A comparative characterization was conducted of the physiological and biochemical performance of seedlings of six OxG hybrids grown in hydroponics. Gas exchange, vegetative growth, protein, sugar and photosynthetic pigment content, and antioxidant system activity were determined. With the exception of gas exchange, the other variables showed significant differences between materials. The 'U1273' and 'U1737' materials showed greater vegetative growth with no expression of biochemical traits, while the 'U1914' and 'U1990' materials showed high levels of reducing and total sugars, photosynthetic pigments, and antioxidant system activities, characteristics that could confer them adaptation to stress conditions. With the standardized hydroponics technique, the optimal conditions for the growth of seedlings were ensured, the differences between materials were established, so those with promising features from the physiological and biochemical standpoint were identified. Finally, it could be used to study in a simple, fast, clean and inexpensive way, the effect of levels and sources of mineral nutrients on the growth and development of oil palm.

Keywords: adaptation, growth, nutrient solution, plant breeding, stress.

RESUMEN

El híbrido interespecífico *Elaeis oleifera* x *Elaeis guineensis* (OxG) es una alternativa para mejorar la competitividad y sostenibilidad de la agroindustria de la palma de aceite latinoamericana, debido a su resistencia parcial a enfermedades letales y a que su aceite es de muy alta calidad. Se realizó la caracterización comparativa del desempeño fisiológico y bioquímico de seis híbridos OxG crecidos en medio hidropónico. Se hicieron determinaciones de intercambio de gases, crecimiento vegetativo, proteínas, azúcares, contenido de pigmentos fotosintéticos y actividad del sistema antioxidante enzimático. Con excepción de las variables

de intercambio de gases, las otras variables mostraron diferencias significativas entre materiales. Los materiales 'U1273' y 'U1737' mostraron mayor crecimiento vegetativo sin expresar cualidades desde el punto de vista bioquímico, mientras los materiales 'U1914' y 'U1990' mostraron altos niveles de azúcares totales y reductores, compuestos fotosintéticos y actividades del sistema antioxidante, características que podrían conferirles adaptación a condiciones de estrés.

Palabras clave: adaptación, crecimiento, estrés, mejoramiento de plantas, solución nutritiva.

INTRODUCTION

Oil palm OxG interspecific hybrids (Arecaceae) result from the cross between two species of economic importance for the oil palm agro-industry in the world, *Elaeis oleifera*, native to the American continent, and pollen of *Elaeis guineensis*, native to Central and West Africa (Rey *et al.*, 2004). These hybrids exhibit intermediate traits compared to the parent species and show hybrid vigor for some traits of agronomic interest that offer great potential for improving the competitiveness and sustainability of the crop, which produces seven times more oil per hectare than following oilseed crop. From the production perspective, the advantages are: slow stem growth (20 cm.year⁻¹ on average) which means a longer useful life of the plantation up 30 years; its partial resistance to the bud rot disease, which is perhaps the greatest threat to the oil palm industry in the Americas (Torres *et al.*, 2010); delayed degradation of the fruit and lower formation of free fatty acids, which translates into a better stability of the fruit after harvest and lower percentage of acidity (less than 2 %) (Corley and Tinker, 2003); high productivity (28-33 t of Fresh fruit bunches·ha⁻¹year⁻¹ with an oil extraction rate between 18% and 19%), which ensures high incomes (Torres *et al.*, 2004); and, the best oil composition in terms of iodine index (68-70) and content of antioxidants such as carotenes, tocopherols and tocotrienols (Corley and Tinker, 2003; Rocha *et al.*, 2006). Therefore, the planting of OxG hybrid materials has been intensified recently in Colombia and Ecuador, at a rate close to 12 %.

Moreover, hydroponics has become an alternative to commercial production of crops for its high efficiency and asepsis. It is

also a very important tool in breeding programs for selecting materials tolerant, for example, to metal toxicity or with important efficiencies in the use of nutrients, so that those differences can be used as practical and efficient criteria for the selection and improvement of the crops (Ayala and Gómez, 2000). In addition, the production in nutrient solutions, under controlled conditions is an option to solve fertilization and irrigation problems, to make efficient use of nutrients and water, and the possibility of changing the composition of the mixture according to the requirements for growth or research (Lara, 1999). However, very few works have been focused on the study of nutrition and the physiological and biochemical performances of the oil palm (*Elaeis guineensis* or OxG interspecific hybrid), and in particular, issues such as deficiencies and toxicities of nutrients have been little explored neither in commercial studies nor in research. So, this research seeks to characterize the physiological and biochemical behavior of six oil palm hybrid materials grown in hydroponics, as part of the standardization of a technique to study later the effect of levels and sources of mineral nutrients on the growth and development of the oil palm in an easy, quick, controlled, clean and inexpensive way.

MATERIALS AND METHODS

The study was carried out in the "Palmar de La Vizcaína" experimental field in Barrancabermeja, Santander (Colombia), at an altitude of 125 meters above sea level, average temperature of 34 °C, relative humidity of 70,5 %, an annual rainfall of 2.852 mm, agroecological conditions that correspond to a Tropical Moist Forest life zone (TMF, Holdridge).

Seeds of six hybrid materials OxG were evaluated. The female parent (*E. oleifera*) was the same, and the pollen (*E. guineensis*) came from four different sources (Table 1). Germination of the seeds was undertaken in sand and after 20 days, seedlings with suitable development were selected and taken to a mesh house and kept under 60 % shading, in polystyrene containers (8 L) with a Hoagland and Arnon nutrient solution (Jones, 2005) at half the original concentration: 3 mM KNO₃, 2 mM Ca(NO₃)₂·4H₂O, 1 mM MgSO₄·7H₂O, 0,5 mM NH₄H₂(PO₄), 0,023 mM H₃BO₃, 5 μM MnCl₂·4H₂O, 0,15 μM CuSO₄·5H₂O, 0,4 μM ZnSO₄·7H₂O, 0,05 μM Na₂MoO₄·2H₂O, and

Table 1. Identity of the interspecific OxG hybrid materials evaluated

Material	Egg		Pollen	
	Origin	Code	Origin	Code
'U1273'	Oleífera	3563	Mongana x Nifor	2012
'U1737'	Oleífera	3557	Mongana	1667
'U1757'	Oleífera	3531	Mongana x Nifor	2012
'U1859'	Oleífera	3563	Avros x Djongo	7092
'U1914'	Oleífera	3531	Mongana	1667
'U1990'	Oleífera	3531	Congo mixto	1640

0,05 mM of a high performance iron chelate. The solution was renewed every eight days, and its pH was monitored every two days and it was kept constant ($4,4 \pm 0,1$) by adding sodium hydroxide (NaOH 1 %) or hydrochloric acid (HCl 0,05 M).

After 120 days keeping the seedlings in a nutrient solution, they were harvested, and the variables of vegetative growth, gas exchange, and biochemical answer were recorded. The height and the diameter of the bulb were measured with a caliper. The first one, from the root insertion point up to the petiole insertion point, and the diameter at the thickest part of the bulb. The number of fully expanded leaves (forked or pinnate) was counted. The leaf area of each seedling was determined using a LI - 3100 scanner (LICOR Inc., Nebraska - USA). Roots and aerial parts were washed with distilled water and oven-dried at 85 °C for 24 hours, and the dry weight was recorded with an electronic scale. Gas exchange measurements like photosynthesis rate, stomatal conductance, and extrinsic water use efficiency (WUE_E) were made on leaf number three, using the portable photosynthesis system LI - 6400 (LICOR Inc., Nebraska - USA), from 8:00 to 11:30 a.m. For these determinations, leaf temperature was kept constant at 30 °C, the CO₂ concentration in the chamber at 400 $\mu\text{mol mol}^{-1}$, the saturation water vapor pressure at 2,5 kPa, photosynthetic active radiation at 1.000 $\mu\text{mol photon}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and a maximum coefficient of variation (CV) of 3 %.

Leaf number three was directly cut and stored at -80 °C, then it was macerated (without midrib) with liquid nitrogen until obtained a fine powder which was keep at -80 °C up to the biochemical determinations using the Synergy MxBioTek system (BIOTEK Instruments, Inc., Winooski - USA). Total sugar content (TSC) and reducing sugar content (RSC) were determined on 15 mg of fresh leaf tissue according to Dubois *et al.* (1956), and Somogyi (1952), respectively. Total leaf protein content (LP) was carried out on 15 mg of fresh tissue using the Bradford method (Bradford, 1976). On 15 mg of fresh leaf tissue extraction was performed the total chlorophyll and carotenoid content with 80 % acetone (v/v) at -20 °C, according to Lichtenthaler and Buschmann (2001). Extraction of catalase and peroxidase was performed on 250 mg of fresh

tissue with 50 mM phosphate buffer, 3 % PVP-40, pH 6,8. The catalase activity (CAT-EC.1.11.1.6) and peroxidase activity (POD-EC.1.11.7.1) were determined by permanganometric method (Ulrich, 1974) and O-dianisidine method (Kireyko *et al.*, 2006) respectively. Extractions of ascorbate peroxidase and glutathione reductase were carried out on 500 mg of fresh tissue with 50 mM Tris-HCl 5,10 μM EDTA-Na₂ pH 7,6. The ascorbate peroxidase activity (APX-EC.1.11.1.11) and glutathione reductase activity (GR-E.C. 1.6.4.2) were performed using spectrophotometric assays (Nakano and Asada, 1981; Yannarelli *et al.*, 2007).

Seedlings were distributed in a complete random design, with five replications. The experimental unit consisted of four seedlings. The generated data were subjected to an analysis of variance and the mean comparison was made by Tukey's test, using the SAS statistical software® version 9.1 (SAS Institute Inc., North Carolina - USA).

RESULTS

Gas exchange variables (photosynthetic rate, stomatal conductance and the extrinsic water use efficiency) showed no significant differences between the hybrid materials, (Table 2), but vegetative growth variables showed statistical differences after four months of evaluation (Table 3). The 'U1273', 'U1737' and 'U1914' materials were the highest, had the widest bulb, and the largest dry matter production. The 'U1990' material had the lowest vegetative growth. As for leaf growth variables, the 'U1273' and 'U1737' materials showed the greatest production of leaves and the largest size of photosynthetic tissue, while the 'U1757', 'U1859' and 'U1990' materials had the lowest values for these variables. The 'U1914' material showed a great growth rate in terms of leaf area, but not in terms of leaf emission.

Total and reducing sugars in leaves showed statistically significant differences among the OxG hybrid materials grown in hydroponics (Table 4). The 'U1990' material had the highest levels of total and reducing sugars, while the 'U1737' material showed the lowest content of total sugar and together with the 'U1757' and 'U1859' materials showed the lowest values of reducing sugars. Chlorophyll and carotenoid

Table 2. Gas exchange of interspecific OxG hybrid materials grown in hydroponics. Values are mean + 1 standard deviation.

Material	Photosynthetic rate ($\mu\text{mol CO}_2\cdot\text{s}^{-1}\cdot\text{m}^{-2}$)	Stomatic conductance ($\text{mmol H}_2\text{O}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$)	WUE_E ($\mu\text{mol CO}_2\cdot\text{mmol}^{-1}\text{ H}_2\text{O}$)
'U1273'	9.69 ± 1.39 a	0.134 ± 0.023 a	3.28 ± 0.49 a
'U1737'	8.90 ± 0.54 a	0.164 ± 0.032 a	3.10 ± 0.40 a
'U1757'	10.03 ± 1.11 a	0.163 ± 0.019 a	3.22 ± 0.32 a
'U1859'	8.68 ± 1.15 a	0.136 ± 0.034 a	2.88 ± 0.18 a
'U1914'	10.08 ± 0.39 a	0.167 ± 0.028 a	3.19 ± 0.34 a
'U1990'	8.59 ± 1.43 a	0.150 ± 0.038 a	2.98 ± 0.37 a

Mean + 1 standard deviation with the same letter are not statistically different. $p < 0.05$ (Tukey).

Table 3. Vegetative growth of interspecific OxG hybrid materials grown in hydroponics. Values are mean + 1 standard deviation.

Material	Height (cm)	Bulb diameter (cm)	Leaf number	Leaf area (cm ²)	Total dry matter (g)
'U1273'	19.0 ± 2.1 a	0.920 ± 0.031 a	5.4 ± 0.6 a	1401.9 ± 228.0 a	13.8 ± 1.9 a
'U1737'	19.5 ± 3.5 a	0.883 ± 0.058 a	5.1 ± 0.3 ab	1186.0 ± 155.0 ab	13.6 ± 3.3 a
'U1757'	17.2 ± 2.1 ab	0.861 ± 0.032 a	4.8 ± 0.3 b	1020.5 ± 90.7 b	12.8 ± 2.2 ab
'U1859'	16.6 ± 1.0 ab	0.806 ± 0.043 ab	4.8 ± 0.4 b	1087.6 ± 112.3 b	12.40 ± 2.8 ab
'U1914'	19.7 ± 3.7 a	0.908 ± 0.106 a	4.8 ± 0.2 b	1343.5 ± 192.7 a	15.0 ± 1.5 a
'U1990'	15.0 ± 1.5 b	0.743 ± 0.043 b	4.7 ± 0.5 b	953.0 ± 201.9 b	10.0 ± 2.2 b

Mean + 1 standard deviation with different letters are significantly different, $p < 0.05$ (Tukey)

Table 4. Sugar content and photosynthetic pigments in the leaf tissue of interspecific OxG hybrid materials grown in hydroponics. Values are mean + 1 standard deviation.

Material	Total sugar content	Reducing sugar content (mg·g ⁻¹ fresh tissue)	Total chlorophyll content	Carotenoid content
'U1273'	8.82 ± 1.01 e	5.26 ± 0.37 c	12.57 ± 0.49 a	0.622 ± 0.285 c
'U1737'	8.05 ± 0.92 f	4.61 ± 0.43 d	12.29 ± 1.12 a	0.954 ± 0.196 b
'U1757'	10.46 ± 0.49 d	4.27 ± 0.41 d	11.33 ± 1.58 b	1.391 ± 0.298 a
'U1859'	13.02 ± 1.69 c	4.46 ± 1.66 d	10.61 ± 0.78 c	0.877 ± 0.416 b
'U1914'	14.15 ± 0.95 b	6.36 ± 0.85 b	10.11 ± 0.89 c	1.637 ± 0.359 a
'U1990'	17.10 ± 1.43 a	7.55 ± 1.04 a	12.48 ± 1.10 a	1.461 ± 0.509 a

Mean + 1 standard deviation with different letters are significantly different, $p < 0.05$ (Tukey).

content showed statistically significant differences between hybrid materials (Table 4). For the total chlorophyll content, the materials were ranked into three groups: the 'U1273', 'U1737' and 'U1990' materials had the highest level, followed by the 'U1757', and finally by the 'U1859' and 'U1914' materials. The carotenoid content recorded three distinguishable levels: the 'U1990', 'U1914' and 'U1757' materials showed the highest values, followed by the 'U1859' and 'U1737', and finally by the 'U1273' materials. The difference between the first and the third group of materials was around three times the content of the metabolites. Protein content and enzymatic activity of the antioxidant system showed statistically significant differences between hybrid materials (Table 5). The 'U1990' and 'U1757' materials had the highest protein content, and the 'U1273' and 'U1737' materials had the lowest. The 'U1990' and 'U1737' materials showed the highest enzymatic activity of catalase, and the 'U1859' material had the lowest activity. The 'U1859' and 'U1990' materials recorded high levels of peroxidase activity and ascorbate peroxidase activity, while the 'U1757' material showed the lowest values of both enzymatic activities. Finally, the 'U1990' material recorded a level of glutathione reductase activity twenty times higher than that of the 'U1273' and 'U1737' materials.

DISCUSSION

Photosynthesis values were lower than those reported by Cristancho *et al.*, (2010) for *Elaeis guineensis* materials under

similar conditions, which implies a differential response of the carbon dioxide assimilation rate in a hydroponic medium, depending on the oil palm genotypes. However, both, the stomatal conductance and the photosynthetic rate showed no statistical differences between materials, suggesting that the stomata of OxG hybrids had a similar regulation for water loss and carbon dioxide intake (Ruiz and Henson, 2002) when grown in a nutrient solution. Also, the OxG materials were able to maintain the CO₂ fixation rate with similar water consumption in a hydroponic medium, which means that they showed the same water use efficiency. Similar values were reported by Samartzidis *et al.*, (2005), in different rose varieties (*Rosa* sp.) growing in hydroponic medium. Also, they did not find any response to the substrate mix and nutrient solution in terms of net photosynthesis, stomatal conductance and water use efficiency.

Despite this, there were differences in the vegetative growth of the hybrid materials. According to Corley and Tinker (2003), the plant growth depends not only on photosynthesis, but the total amount of solar energy available, the degree of interception and absorption of this energy by leaves, the efficient distribution of these assimilates, and the efficiency of carbohydrate conversion to chemical energy. Additionally, Valles *et al.*, (2009), reported that the accumulation of dry matter is determined mainly by the genotype, the age of the crop and the assimilate translocation in the plant and the management. Therefore, assuming that the amount of available solar energy

Table 5. Total protein content and activity of enzymes of the antioxidant system of interspecific OxG hybrid materials grown in hydroponics. Values are mean + 1 standard deviation.

Material	Total soluble protein ($\mu\text{g}\cdot\text{g}^{-1}$ fresh tissue)	CAT activity ($\mu\text{moles H}_2\text{O}_2$ [minute mg protein]) ⁻¹	POD activity (Δ Abs. 436 nm· [minute mg protein]) ⁻¹	APX activity (nmoles oxidized ascorbate [minute mg protein]) ⁻¹	GR activity (nmoles NADPH [minute mg protein]) ⁻¹
'U1273'	43.98 ± 7.38 c	11.96 ± 2.48 c	392.89 ± 39.57 cd	11.51 ± 2.86 e	9.99 ± 2.39 e
'U1737'	43.47 ± 4.48 c	14.84 ± 3.51 ab	402.42 ± 59.48 cd	13.37 ± 1.04 e	10.46 ± 0.78 e
'U1757'	76.85 ± 6.94 a	12.44 ± 0.93 c	348.72 ± 50.40 d	21.56 ± 2.77 d	49.35 ± 6.03 d
'U1859'	58.32 ± 2.09 b	9.64 ± 1.11 d	616.66 ± 58.31 a	60.86 ± 3.72 a	85.42 ± 9.50 c
'U1914'	58.55 ± 17.12 b	13.38 ± 3.43 bc	420.48 ± 95.11 c	36.42 ± 2.70 c	156.82 ± 43.39 b
'U1990'	76.55 ± 22.10 a	16.02 ± 3.95 a	498.25 ± 106.16 b	40.45 ± 6.63 b	218.24 ± 41.63 a

Mean + 1 standard deviation with different letters are significantly different, $p < 0.05$ (Tukey)

is the same for all materials, the 'U1273', 'U1737' and 'U1914' hybrids, that had the highest leaf growth, would be more likely to intercept and absorb the incident solar radiation, as reported by Rodríguez and Cayón (2008), and be more efficient in net assimilation and distribution of photoassimilates for their growth (Corley and Tinker, 2003). The accumulation of biomass per plant obtained after 120 days growing in a nutrient solution was significantly associated with a greater leaf area ($p = 0.53$). This is consistent with the results by Cruz *et al.*, (2005) and Flores *et al.*, (2009) for potato plants (*Solanum tuberosum*) and pepper (*Capsicum annuum*) respectively, grown in greenhouses and hydroponics under different management conditions. They also argue that an increase in leaf area maximizes the interception of radiation and, therefore, the biomass per unit area up to a maximum limit to prevent shading. Also, they stated that for the majority of crop species with a C3 photosynthetic mechanism, such as the oil palm, the largest light interception is achieved with a leaf area index of three to four (Henson, 1990; Samartzidis *et al.*, 2005). Furthermore, the 'U1990' and 'U1914' materials showed advantages in terms of sugar reserves. The importance of maintaining high levels of sugars in leaf tissue lies in a greater adaptability of plants to different types of biotic and abiotic stress (Leyman *et al.*, 2001; Paul *et al.*, 2008). Reports in *Nicotiana tabacum* (Best *et al.*, 2011) suggest that plants with high biosynthesis of trehalose and sucrose have comparative advantages in adaptation to different types of stress, in addition to having improved photoassimilate partitioning and increased growth rates. As for the chlorophyll and carotenoid content, the levels found are similar to those reported by Znidarcic *et al.*, (2011) in *Cichorium intybus*, *Taraxacum officinale*, *Eruca sativa* and *Diplotaxis tenuifolia*. The 'U1990' material showed high levels of both pigments, so, this material would have advantages in regards to photosynthetic processes, the efficiency in the use of captured energy (Gamon and Surfus, 1999; Dolferus *et al.*, 2011), leaf development, biomass accumulation and adaptation to stress conditions (Schwartz and Von Elbe, 1983; Kimura and Rodríguez, 2003; Znidarcic *et al.*, 2011). Also, the 'U1990' material, that

exhibited the highest levels of enzyme activity, could have a metabolic advantage in the regulation and maintenance of adequate reactive oxygen species levels in the chloroplast and mitochondria, as reported before (Anderson *et al.*, 1995; Baier and Dietz, 1997; Wang *et al.*, 1999; Chew *et al.*, 2003; Dewitte and Murray, 2003; Ball *et al.*, 2004). The biosynthesis and early activation of these enzymes can give this material a high index of adaptation to different types of biotic and abiotic stress (Acevedo *et al.*, 2001; Palatnik *et al.*, 2002; Apel and Hirt, 2004), as it is demonstrated by studies in transgenic plants (Sanmartin *et al.*, 2003).

Although, the 'U1990' material had the lowest growth rates, the biochemical characterization suggests that it has interesting traits in terms of osmoprotectant molecule levels, like reducing and total sugars, photosynthetic pigment content and antioxidant enzyme activities, which could give it advantages in adaptation to stress conditions. The 'U1273' and 'U1737' materials that showed a greater vegetative growth rate with no expression of biochemical traits might show a lower response in terms of optimal growth and development under limiting conditions (biotic and/or abiotic) to which the crop is exposed. Meanwhile, the 'U1914' material exhibited high levels of reducing and total sugars, photosynthetic pigments and antioxidant system activity and an outstanding leaf growth in height and accumulation of dry mass. Consequently, it is interesting for a breeding program, which could explore its promising performance.

Finally, the developed hydroponics system, provided high bioavailability of essential elements and ensured optimal conditions for the growth and development of plants, and it made possible to recognizing the differences between the OxG hybrid materials due to the center of origin of their parents or the cross type, as reported by Cadena *et al.*, (2013), identified materials with promising traits from the physiological and biochemical perspective, as well as to establish a dynamic, fast and clean technique for conducting trials on mineral nutrition, metal stress (aluminum, iron, manganese, etc.), root development, etc., issues that remain unexplored in oil palm cultivation.

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REFERENCES

- Acevedo A, Paleo Ad, Federico ML. Catalase deficiency reduces survival and pleiotropically affects agronomic performance in field-grown barley progeny. *Plant Sci.* 2001;160(5):847-855.
- Anderson MD, Prasad TK, Stewart CR. Changes in isozyme profiles of catalase, peroxidase, and glutathione reductase during acclimation to chilling in mesocotyls of maize seedlings. *Plant Physiol.* 1995;109(4):1247-1257.
- Apel K, Hirt H. Reactive oxygen species: metabolism, oxidative stress, and signal transduction. *Annu Rev Plant Biol.* 2004;55:373-399.
- Ayala I, Gómez P. Identificación de variables morfológicas y fisiológicas asociadas con el rendimiento en materiales de palma de aceite (*Elaeis guineensis* Jacq.). *Palmas* 2000;21(4):10-21.
- Baier M, Dietz K. The plant 2-Cys peroxiredoxin BAS1 is a nuclear-encoded chloroplast protein: its expressional regulation, phylogenetic origin, and implications for its specific physiological function in plants. *Plant J.* 1997;12(1):179-190.
- Ball L, Accotto G, Bechtold U, Creissen G, Funck D, Jiménez A, *et al.* Evidence for a direct link between glutathione biosynthesis and stress defense gene expression in *Arabidopsis*. *Plant Cell.* 2004;16(9):2448-2462.
- Best M, Koenig K, McDonald K, Schueller M, Rogers A, FERRIERI R. Inhibition of trehalose breakdown increases new carbon partitioning into cellulosic biomass in *Nicotiana tabacum*. *Carbohydr Res.* 2011;346(5):595-601.
- Bradford M. A rapid and sensitive method for the quantization of micrograms quantities of protein utilizing the principle of protein dye binding. *Anal Biochem.* 1976;72:248-254.
- Cadena T, Prada F, Perea A, Romero H. Lipase activity, mesocarp oil content, and iodine value in oil palm fruits of *Elaeis guineensis*, *Elaeis oleifera*, and the interspecific hybrid OxG (*E. oleifera* x *E. guineensis*). *J Sci Food Agr.* 2013;93(3):674-680.
- Corley R, Tinker P. *The Oil Palm*. 4 Ed. Oxford. Blackwell Science; 2003.
- Chew O, Whelan J, Millar AH. Molecular definition of the ascorbate-glutathione cycle in *Arabidopsis* mitochondria reveals dual targeting of antioxidant defenses in plants. *J Biol Chem.* 2003;278(47):46869-46877.
- Cristancho RJ, Hanafi MM, Syed SR, Rafii MY. Variations in oil palm (*Elaeis guineensis* Jacq.) progeny response to high aluminium concentrations in solution culture. *Plant Biol.* 2010;13(2):33-42.
- Cruz N, Ortiz J, Sánchez F, Mendoza M. Biomasa e índices fisiológicos en chile morrón cultivado en altas densidades. *Rev Fitotec Mex.* 2005;28(3):287-293.
- Dewitte W, Murray J. The plant cell cycle. *Annu Rev Plant Biol.* 2003;54:235-264.
- Dolferus R, Ji X, Richards R. Abiotic stress and control of grain number in cereals. *Plant Sci.* 2011;181(4):331-341.
- Dubois M, Gilles K, Hamilton J, Rebers P, Smith F. Colorimetric method for determination of sugars and related substances. *Anal Chem.* 1956;28(3):350-356.
- Flores R, Sánchez F, Rodríguez J, Colinas M, Mora R, Lozoya H. Densidad de población en cultivo hidropónico para la producción de tubérculo-semilla de papa (*Solanum tuberosum* L.). *Rev Chapingo Ser hortic.* 2009;15(3):251-258.
- Gamon J, Surfus J. Assessing leaf pigment content with a reflectometer. *New Phytol.* 1999;143(1):105-117.
- Henson IE. Photosynthesis and source-sink relationships in oil palm (*Elaeis guineensis*). *Trans Malay Soc Plant Physiol.* 1990;2(1):165-171.
- Kimura M, Rodríguez D. Carotenoid composition of hydroponic leafy vegetables. *J Agric Food Chem.* 2003;51(9):2603-2607.
- Kireyko A, Veselova I, Shekhovtsova TN. Mechanisms of peroxidase oxidation of o-dianisidine, 3,3',5,5'-tetramethylbenzidine, and o-phenylenediamine in the presence of sodium dodecyl sulfate. *Russ J Bioorganic Chem.* 2006;32(1):71-77.
- Jones B. *Hidroponics: A practical guide for the soilless grower*. Ed 2. Boca Raton: CRC Press; 2005.
- Lara A. Manejo de la solución nutritiva en la producción de tomate en hidroponía. *Terra.* 1999;17(3):221-229.
- Leyman B, Van Dijk P, Thevelein J. An unexpected plethora of trehalose biosynthesis genes in *Arabidopsis thaliana*. *Trends Plant Sci.* 2001;6(11):510-513.
- Lichtenthaler H, Buschmann C. Chlorophylls and carotenoids - Measurement and characterization by UV-VIS. In: Wrolstad R, Editor in Chief. *Current Protocols in Food Analytical Chemistry*. Madison: John Wiley & Sons; 2001. p. 14117-14234.
- Nakano Y, Asada K. Hydrogen peroxide is scavenged by ascorbate specific peroxidase in spinach chloroplasts. *Plant Cell Physiol.* 1981;22(5):867-880.
- Palatnik J, Valle E, Federico M, Gómez L, Melchiorre M, Díaz-Paleo A, *et al.* Status of antioxidant metabolites and enzymes in a catalase-deficient mutant of barley (*Hordeum vulgare* L.). *Plant Sci.* 2002;162(3):363-371.
- Paul M, Primavesi J, Jhureea L, Zhang Y. Trehalose metabolism and signaling. *Annu Rev Plant Biol.* 2008;59:417-441.
- Rey L, Gómez P, Ayala I, Delgado W, Rocha P. Colecciones genéticas de palma de aceite *Elaeis guineensis* (Jacq.) y *Elaeis oleifera* (H.B.K.) de Cenipalma: Características de importancia para el sector palmicultor. *Palmas.* 2004;25(4):39-48.

- Rocha P, Prada F, Rey L, Ayala I. Caracterización bioquímica parcial de la colección de *Elaeis oleifera* de Cenipalma proveniente de la Amazonía colombiana. *Palmas* 2006;27(3):35-44.
- Rodríguez P, Cayón G. Efecto de *Mycosphaerella fijiensis* sobre la fisiología de la hoja de banano. *Agron Colomb*. 2008;26(2):256-265.
- Ruiz R, Henson I. Photosynthesis and stomatal conductance of oil palm in Colombia: some initial observations. *The Planter*. 2002;78(915):301-308.
- Samartzidis C, Awada T, Maloupa E, Radoglou K, Constantinidou H. Rose productivity and physiological responses to different substrates for soil-less culture. *Sci Hortic*. 2005;106(2):203-212.
- Sanmartin M, Drogoudi PA, Lyons T, Pateraki I, Barnes J, Kanellis AK. Over-expression of ascorbate oxidase in the apoplast of transgenic tobacco results in altered ascorbate and glutathione redox states and increased sensitivity to ozone. *Planta*. 2003;216(6):918-928.
- Schwartz S, Von Elbe J. Kinetics of chlorophyll degradation to pyropheophytin in vegetables. *J Food Sci*. 1983;48(4):1303-1306.
- Somogyi M. Notes of sugar determination. *J Biol Chem*. 1952;195:19-23.
- Torres M, Rey L, Gelves F, Santacruz L. Evaluación del comportamiento de los híbridos interespecíficos *Elaeis oleifera* x *Elaeis guineensis* en la plantación Guaicaramo S.A. *Palmas*. 2004;25(4):351-357.
- Torres G, Sarria G, Varon F, Coffey M, Elliot M, Martinez G. First report of bud rot caused by *Phytophthora palmivora* on African oil palm in Colombia. *Plant Dis*. 2010;94(9):1163.
- Ulrich B. *Methods in Enzymology*. New York: Editorial Academic Press; 1974.
- Valles G, Lugo J, Rodríguez Z, Díaz L. Efecto del sustrato y la distancia de siembra entre plantas sobre el crecimiento de plantas de pimentón (*Capsicum annum* L.) en un sistema hidropónico sin cobertura. *Rev Fac Agron*. 2009;26:159-178.
- Wang J, Zhang H, Allen R. Over expression of an *Arabidopsis* peroxisomal ascorbate peroxidase gene in tobacco increases protection against oxidative stress. *Plant Cell Physiol*. 1999;40(7):725-732.
- Yannarelli GG, Fernández-Alvarez AJ, Santa-Cruz DM, Tomaro ML. Glutathione reductase activity and isoforms in leaves and roots of wheat plants subjected to cadmium stress. *Phytochemistry*. 2007;68(4):505-512.
- Znidarcic D, Ban D, Sircelj H. Carotenoid and chlorophyll composition of commonly consumed leafy vegetables in Mediterranean countries. *Food Chem*. 2011;129(3):1164-1168.

