Effects of solar eclipse on photosynthesis of *Portulaca oleracea* and *Phyla nodiflora* in coastal wild conditions

K. Sambandan^{1*}, K. Seethala Devi¹, S. Santosh Kumar², M.Nancharaiah³ and N. Dhatchanamoorthy¹

¹Post Graduate Department of Plant Science, Avvaiyar Government College for Women, Karaikal – 609 602, U.T of Puducherry, India ²Department of Physics, Avvaiyar Government College for Women, Karaikal – 609 602, U.T of Puducherry, India ³Cyclone Data Radar Station, Karaikal – 609 602, U.T of Puducherry, India

Abstract

The total solar eclipse provided a unique opportunity to understand the effects of solar radiation on the biosphere. The present study attempts to record meteorological parameters and to compare chlorophyll contents of *Portulaca oleracea* and *Phyla nodiflora* in coastal wild conditions during total solar eclipse on July 22, 2009. Changes in meteorological parameters such as temperature by 0.5°C, relative humidity by 4% and light intensity around 100 lux were set to be low during eclipse day when compared to that of corresponding week. Minor changes were also observed in the wind speed and direction during solar eclipse day. Mature leaves of *Portulaca oleracea* and *Phyla nodiflora* from coastal wild conditions were collected and analysed for total chlorophyll, chlorophyll a, chlorophyll b and carotinoid contents at various time intervals during solar eclipse day and previous days. Chlorophyll levels were decreased slightly during solar eclipse day, whereas carotinoid levels were increased marginally in both the plant species. Solar radiation and its photochemical phases during eclipse day are responsible for the observed reduction in photosynthetic rates of wild plants.

Keywords: Solar eclipse, Photosynthesis, Phyla nodiflora, Portulaca oleracea, Coastal wild plants

INTRODUCTION

Eclipses, either solar or lunar, have been attracting the interest of people since ancient years. In modern times, solar eclipses still trigger the attention of scientists, and it is used for objectively testing physical and biological hypotheses. However, solar eclipses have also been the object of special focus by various experts from different research fields. A solar eclipse constitutes a challenge for researchers to study the response of the lower atmosphere to abrupt changes in the incident solar radiation. The response of the earth's environment to the abrupt and short-time disturbance in the radiation, and in consequence the thermal balance of the atmosphere has been the subject of many environmental studies during the last century.

The environmental effects of a solar eclipse have been mainly focused on meteorological parameters [1], photochemistry [2], boundary layer physics [3], total columnar ozone [4], gravity waves [5], ionospheric parameters [6] and also plants [7] and animals [8]. Temperature, relative humidity, wind and cloudiness are among the most common meteorological parameters measured in experimental campaigns during solar eclipses [9-12].

In the biosphere, it is found that various plant species respond differently to the induced changes in solar radiation, allowing the use of certain species as indices for future climate changes. The effects

Received: Dec 03, 2011; Revised: Jan 12, 2012; Accepted: Feb 06, 2012.

*Corresponding Author

K. Sambandan

Post Graduate Department of Plant Science, Avvaiyar Government College for Women, Karaikal – 609 602, U.T of Puducherry, India

Tel: +91-9489-260386; Fax: +91-4368-226380 Email: sambandhan@gmail.com of solar eclipses on the behaviour of living organisms have been the subject of many observations in the past. During the solar eclipse of 1932, plant behaviour was studied with the help of stomatal movements of grey birch trees [7]. Two Polish zoologists were the first to observe the behaviour of mammals, birds, and insects during seven eclipses between 1954 and 1975 [8]. More recent data have shown that birds behave as they normally do at sunset [13], animals alter their behaviour [14] and some planktonic crustacea are vertically redistributed [15-16].

Kazantzidis and others [17] with the help of Greek UV monitoring network, investigated the variability of the ultraviolet and the photosynthetically active radiation (PAR) during the total solar eclipse. They showed that radiations at shorter wavelengths are generally influenced more by the eclipse. Various solar eclipse effects on plants mainly related to the abrupt solar light "switch off" such as transient aberrations in the chromosomal structure of root meristems and a delaying seed germination, effects on photosynthesis and evapo-transpiration of crop plants etc, have been reported by Gerasopoulos and others [18]. In order to put insight, the mechanisms involved in the effects of solar eclipses on photosynthesis and stomatal behaviour, they also reported that photosynthetic rates decreased in seven field grown cereal and leguminous crops during the eclipse, in accordance with the PAR. Comparison of the photosynthetic activity drop during the eclipse with the respective diurnal cycle showed that the effects resemble those obtained at dusk or under dense cloudiness.

The diurnal course of stomatal conductance (gs) followed a normal pattern for mesophytic crop species, with higher values during solar eclipse and steadily declining for the next two to three hours and remaining stable thereafter. It has shown that solar irradiance was not the factor directly affecting the course of gs during the eclipse. They concluded that since solar irradiance attenuation has not induced stomatal closure and did not block CO_2 uptake by

plants. Other endogenous factors may also be responsible for the observed fall in photosynthetic rates.

A decade before, on 11 August 1999, we had an opportunity of witnessing a total solar eclipse from India. After a long wait we again witnessed a total solar eclipse on 22 July 2009, which was visible in many parts of India. This eclipse could be considered the longest total solar eclipse till 2114. In general, eclipse effects on plants are expected to be related to the light limitation experienced during the phenomenon. Although fluctuating conditions of light are a common feature for natural habitats through transitional light flecks in canopies, changing cloudiness, diurnal periods of light and dusk [19-20], the sudden drop in solar irradiance during a solar eclipse provides a challenge for investigating its related impacts on plant behaviour. Observations have shown that a drop of sap flow velocity in a number of plants was related to solar eclipses [21-23]. In this situation, the aim of the present study is to compare chlorophyll contents of Portulaca oleracea and Phyla nodiflora in coastal wild conditions during total solar eclipse in July 22, 2009.

MATERIALS AND METHODS

Mature leaves of *Portulaca oleracea* and *Phyla nodiflora* were freshly collected from coastal vegetation of Karaikal (U.T of Puducherry) from 20-07-2009 to 24-07-2009 at 6.30 AM in the morning, whereas on total solar eclipse day (22-07-2009) collections from 5.00 AM to 7.30 AM in every 30 minutes intervals were made. Each leaf sample was washed thoroughly with distilled water and weighed 20 g, and chlorophyll content was extracted and determined spectrophotometrically according to a procedure described by Jayaraman [24] and results were given as mg chl/g leaf fresh weight. Chlorophyll content was assayed with UV-visible spectrophotometer (Systronics UV-Vis Model 2201). Each sample was measured three times in the same conditions and results were given on an average of three value.

Meteorological parameters such as temperature, relative humidity, visibility, wind speed, wind degree and light intensity were also measured using standard procedures. Usually, temperature, humidity and wind measurements are the variables that are measured by a thermometer, hygrometer and anemometer

RESULTS

Meteorological parameters were recorded from 20-07-2009 to 24-09-2009 at 6.30 AM including solar eclipse day (22-07-2009). Temperature (°C), Relative humidity (%), Wind Speed (Kmph), Wind Degree and Light intensity (Lux) were tabulated as in Table-1. Temperature was recorded for whole week and minimum temperature (27.3 °C) was recorded at eclipse day, previous day of eclipse (27.8 °C) and next day of eclipse (28.1 °C) at morning 6.30 AM. More than 0.5 °C changes were observed during the eclipse day. Relative humidity was measured previous day of Eclipse (69 %), during eclipse day (65%) and next day of eclipse (69 %). Variation in relative humidity of 4 per cent was considered lower than normal values.

Wind speed and wind degree also changed during eclipse day. Wind speed recorded 12 km per hour on eclipse day, 16 km per hour on previous day and 15 km per hour on next day of eclipse. There is minor reduction is observed in the wind speed during solar eclipse day. Wind degree was recorded as 230° during eclipse day but it was recorded as 250° on the previous and the next day of solar eclipse. Light intensity was measured using lux meter at 6.30 AM during the whole week centered on solar eclipse. Light intensity (100 lux) was also set to be low during the eclipse compared to that of whole week. Comparison of meteorological parameters during solar eclipse day at different time intervals also was recorded as in Table-2 and considerable variations of parameters were found during eclipse period with other periods.

Chlorophyll contents were analysed in *Portulaca oleracea* (Table 3; Fig. 1) and *Phyla nodiflora* (Table 4; Fig. 4) grown in coastal wild conditions. Mature leaves of these plants were collected and analysed for total chlorophyll, chlorophyll-a, chlorophyll-b and carotinoid contents at various time intervals during solar eclipse day (22-07-2009) and previous day i.e normal day (21-07-2009). Chlorophyll levels were decreased slightly during solar eclipse, whereas carotinoid levels were increased marginally in both the plant species.

Date	Time	Temperature (C°)	Relative Humidity (%)	Wind speed (Kmph)	Wind Degree	Light intensity (in Lux)
20-07-2009	6.30 AM	28.0	68	14	250	2026
21-07-2009	6.30 AM	27.8	69	16	250	1819
22-07-2009*	6.30 AM	27.2	65	12	230	1002
23-07-2009	6.30 AM	28.1	69	14	250	2704
24-07-2009	6.30 AM	28.2	70	16	250	2580

Table 1. Comparison of meteorological parameters during solar eclipse day with normal days

* - Eclipse day

Table 2. Comparison of meteorological parameters during solar eclipse day at different time periods

Time	Temperature (C°)	Relative Humidity (%)	Wind speed (Kmph)	Wind Degree	Light intensity (in Lux)
5.00 AM	27.2	65	16	250	
5.30 AM	27.4	66	14	230	10
6.00 AM	27.6	66	14	230	229
6.30 AM	27.2	65	12	230	967
7.00 AM	27.6	65	14	230	9660
7.30 AM	29.1	69	14	230	6720

	Day	5.00 AM	5.30 AM	6.00 AM	6.30 AM	7.00 AM	7.30 AM	8.00 AM
Total Chlorophyll	Eclipse Day	0.104	0.116	0.128	0.133	0.135	0.141	0.158
	Normal Day	0.102	0.127	0.133	0.141	0.147	0.154	0.156
Chlorophyll-a	Eclipse Day	0.061	0.063	0.071	0.065	0.067	0.073	0.106
	Normal Day	0.064	0.068	0.078	0.082	0.089	0.098	0.112
Chlorophyll-b	Eclipse Day	0.078	0.081	0.081	0.078	0.076	0.087	0.104
	Normal Day	0.075	0.081	0.092	0.096	0.102	0.113	0.114
Carotinoid	Eclipse Day	0.740	0.910	1.190	1.220	2.010	2.060	2.090
	Normal Day	0.640	0.790	0.98	0.990	1.510	1.790	1.860

Table 3. Changes in total chlorophyll, chlorophyll-b and carotinoid levels of *Portulaca oleracea* mg/g (Fresh weight); Results are mean values of five replicates

Table	4. Changes in total	chlorophyll.	chlorophyll-a.	chlorophvll-b an	d carotinoid levels o	of Phyla nodiflora	ma/a (Fres	h weiaht):	Results are mean	values of five replicates
	J					,	0.0 1	- 0 - / /		

	Day	5.00 AM	5.30 AM	6.00 AM	6.30 AM	7.00 AM	7.30 AM	8.00 AM
Total Chlorophyll	Eclipse Day	0.135	0.140	0.135	0.130	0.144	0.149	0.171
(mg/g FW)	Normal Day	0.132	0.139	0.144	0.151	0.156	0.171	0.182
Chlorophyll a	Eclipse Day	0.066	0.066	0.071	0.072	0.077	0.86	0.96
(mg/g FW)	Normal Day	0.064	0.068	0.078	0.082	0.089	0.098	0.109
Chlorophyll b	Eclipse Day	0.086	0.090	0.094	0.095	0.096	0.099	0.112
(mg/g FW)	Normal Day	0.082	0.089	0.099	0.108	0.116	0.121	0.125
Carotinoid	Eclipse Day	0.750	0.773	0.850	0.890	0.912	0.970	0.998
(mg/g FW)	Normal Day	0.723	0.734	0.759	0.815	0.842	0.890	0.916



Fig 1. Chlorophyll and Carotinoid levels of Portulaca oleracea during eclipse and normal Period.

Time		Wave length (nm)											
	360	400	440	480	500	560	600	640	645	663	680	720	
5.30 AM	1.04	1.28	1.53	1.12	0.29	0.38	0.64	0.94	1.06	1.63	0.68	0.05	
6.30 AM	0.72	1.75	1.97	1.14	0.31	0.41	0.65	0.89	1.02	1.62	0.77	0.11	
7.30 AM	1.07	1.98	1.45	1.33	0.33	0.39	0.63	0.91	1.02	1.57	0.66	0.04	





Fig 2. Chlorophyll and Carotinoid levels of Phyla nodiflora during eclipse and normal period

Table 6. Action spectrum of Phyla nodiflora leaves during eclipse day

Time	Wave length (nm)											
	360	400	440	480	500	560	600	640	645	663	680	720
5.30 AM	1.31	1.76	1.67	1.12	0.23	0.34	0.65	1.04	1.18	1.55	0.54	0.01
6.30 AM	1.09	1.83	1.94	1.11	025	0.36	0.67	1.07	1.25	1.65	0.62	0.03
7.30 AM	1.43	1.88	1.56	1.07	0.25	0.35	0.62	0.99	1.16	1.56	0.56	0.04



Fig.3. Action spectrum of Portulaca oleracea during eclipse day



Fig 4. Action spectrum of Phyla nodiflora during eclipse day

Leaf chlorophyll concentration is strongly affected by numerous external factors including light intensity. Action spectrum of *Portulaca oleracea* and *Phyla nodiflora* also varied at 360 to 500 nm on eclipse day at various time intervals (Table 5 & 6; Fig. 3 & 4). Chlorophyll contents were decreased at 360 to 500 nm when compared to previous day results but steadily increased within an hour. Carotinoids were increased marginally during solar eclipse but adjusted with increasing light intensity.

DISCUSSION

Solar eclipses have been the object of special focus by various experts from different research fields. The total solar eclipse provided a unique opportunity to understand the effects of solar radiation on the biosphere. Temperature, relative humidity, wind and cloudiness are among the most common meteorological parameters measured and observed in experimental campaigns during solar eclipses [9-12], [25]. In the present study, changes in meteorological parameters such as temperature reduced by 0.5°C, relative humidity lowered by 4% and light intensity around 100 lux are observed during eclipse day when compared to that of whole week. Although the results of most meteorological studies provide similar patterns of temperature changes, the precise temperature drop may differ depending on several factors such as timing of the eclipse, synoptic situation, surrounding environment, percentage of sun occultation etc.

Meteorological observations at the different sites within Greek domain showed that the reduction in the incoming shortwave solar radiation was dramatic and ranged from 100% to 75%, depending on the obscuration percentage and local cloudiness. According to Gerasopoulos *et al* [18] Temperature drop during solar eclipse was not determined by the obscuration percentage, but by the surrounding environment and the local conditions. An "eclipse wind" has been also emerged throughout eclipse period [12], although in some cases, it could be also related to subjective perception of a pronounced wind chill effect [9]. According to recent observations, wind speed was decreased during solar eclipse time [10-11]. In the present work, changes were also observed in the wind speed and direction during solar eclipse day.

Photosynthesis is a key for dry matter production, photosynthetic efficiency and increasing productivity [26]. Of all aspects of plant metabolism, photosynthesis shows the most prominent variation influence by the immediate environment [27]. Chlorophyll-a and chlorophyll-b and carotinoid concentrations correlate to the photosynthetic potential of plants and subsequently to indicate physiological and metabolic status [28-30]. Estimates of pigment concentrations may provide evaluative information about the spatial and temporal dynamics of plant stress [31-33]. In the

present study, changes in chlorophyll contents were recorded in the *Portulaca oleracea* and *Phyla nodiflora* in coastal wild conditions during solar eclipse day.

Absorbtion of light in excess of photosynthetic utilization by green plant leaves may lead to a reduction in the potential efficiency of photosystem II, which persist in low or darkness and is regarded as the major cause of photoinhibition of photosynthesis [34]. It has been shown for many plant species that photo inhibition of photosynthesis does occur under natural conditions [35]. Photosynthesis could be regulated either through the membrane bound light reactions and/or through the more loosely membrane associated K reactions involved in CO_2 fixation. Observations of conformational changes in chloroplast shapes or thylakoid orientation [36, 37], has based on the shapes of photosynthesis-irradiance curves.

Chlorophyll accumulation is rapid at high temperature under all conditions of light intensity. At low temperature and particularly in combination with light intensity (3000-4500 ft), the accumulation both of chlorophyll and carotene is inhibited. Carotenoids are known to participate in the capture and transfer of light energy. They also function as important light screening pigment, and play a role in protecting chlorophyll and other porphyrins such as catalase and cytochrome from photo-destruction [38-40]. Once chlorophyll has formed, and it would be protected from rapid photo-destruction. In the present study, chlorophyll contents were decreased at 360 to 500 nm when compared to previous day results but steadily increased within an hour. Carotinoids were increased marginally during solar eclipse but adjusted with increasing light intensity. Seybold and Falk [41] concluded that there was no daily change in the chlorophyll content of mature leaves but some variation in overall chlorophyll content occurred in young leaves. The present investigation asserts that variations in chlorophyll content do exist in different time intervals. Chlorophyll levels were decreased slightly during solar eclipse day, whereas carotinoid levels were increased marginally in both the plant species.

CONCLUSION

Variations in the photochemical phases of solar light during solar eclipse may be responsible for the observed depression in photosynthetic rates. In the present study, the observations on changes in the temperature, relative humidity, radiation, wind speed during the solar eclipse period. Present study also showed that the chlorophyll contents were decreased during solar eclipse day at 360 to 500 nm when compared to normal day results but steadily increased within an hour. Carotinoids were increased marginally during solar eclipse but adjusted with increasing light intensity. Chlorophyll concentration before and during solar eclipse day have to be taken under serious consideration for planning solar eclipse related research in the future.

ACKNOWLEDGEMENT

The authors are grateful to the Principal, Avvaiyar Government College for Women, Karaikal, U.T of Puducherry, India for providing facilities and encouragement throughout the study.

REFERENCES

- Anderson, R. C., D. R. Keefer and O. E. Myers. 1972. Atmospheric pressure and temperature changes during the 7 March 1970 solar eclipse. *J. Atmos. Sci.* 29:583–587.
- [2] Srivastava, G. P., M. P. M. Pakkir and R. R. Balwalli. 1982. Ozone concentration measurements near the ground at Raichur during the solar eclipse of 1980. *Proc. Ind. Nat. Sci. Aca. A.* 48:138–142.
- [3] Antonia, R. A., A. J. Chambers, D. Phong-Anant, S. Rajagopalan and K.R. Sreenivasan. 1979. Response of atmospheric surface layer turbulence to a partial solar eclipse. *J. Geophys. Res.* 4:1689–1692.
- [4] Kawabata, Y. 1937. Spectrographic observation on the amount of ozone at the total solar eclipse of 15 February 1961. J. Astron. Geophys.14:1–3.
- [5] Chimonas, G. and C. O. Hines. 1970. Atmospheric gravity waves induced by a solar eclipse. J. Geophys. Res. 75:875.
- [6] Klobuchar J. A. and H. E. Whitney. 1965. Ionospheric electron content measurements during a Solar 15 Eclipse. J. Geophys. Res. 70:1254–1257.
- [7] Deen, J. L. and M. H. Bruner. 1933. The effect of the 1932 eclipse upon the width of stomatal openings in gray birch. *Ecology*. 14:76–77.
- [8] Zirker, J. B. 1995. Total Eclipses of the Sun, Princeton University Press, New Jersey, USA, pp 228.
- [9] Anderson, J. 1999. Meteorological changes during a solar eclipse. Weather. 54:207–215.
- [10]Fernandez, W., V.Castro and H. Hidalgo. 1993. Air temperature and wind changes in Costa Rica during the total solar eclipse of 11 July 1991. *Earth Moon Planets*. 63:133–147.
- [11]Fernandez, W., H. Hidalgo, G. Coronel and E. Morales. 1996. Changes in meteorological variables 20 15 in Coronel Oviedo, Paraguay, during the total solar eclipse of 3 November 1994. *Earth Moon Planets*. 74:49–59.
- [12]Aplin, K. L. and R. G. Harrison. 2002. Meteorological effects of the eclipse of 11 August 1999 in cloudy and clear conditions. *Proc. R. Soc. Lond. A.* 10:1042-1050.
- [13]Tramer, E. J. 2000. Bird behavior during a total solar eclipse. *Wilson Bull*. 112:432–432.
- [14] Jennings, S., R. Bustamante, H. K. Collins and J. Mallinson. 1998. Reef fish behaviour during a total solar eclipse at Pinta Island, Galapagos. J. Fish Biol. 53:683–686.

- [15] Vecchione, M., R. S. Maples and R. Donahoe. 1987. Changes in chlorophyll a concentrations in a shallow water column during a solar eclipse. *Contrib. Mar. Sci.* 29: 37–44.
- [16]Giroud, C. and G. Balvay. 1999. The solar eclipse and the migration of some planktonic crustacea in Lake Geneva. Arch. Sci. 52:199–208.
- [17]Kazadzis, S., A. Bais, M. Blumthaler, A. Webb, N. Kouremeti, R. Kift, B. Schallhart and A. Kazantzidis. 2007. Effects of total solar eclipse of 29 March 2006 on surface radiation. *Atmos. Chem. Phys.* 7:5775–5783.
- [18]Gerasopoulos, E., C. S. Zerefos, I. Tsagouri, D. Founda, V. Amiridis, A. F. Bais, A. Belehaki, N. Christou, G. Economou, M. Kanakidou, A. Karamanos, M. Petrakis and P. Zanis. 2007. The Total Solar Eclipse of March 2006: overview. *Atmos. Chem. Phys. Discuss.* 7:663–704
- [19]Schulze, E. D. and A. E. Hall. 1982. Stomatal responses, water loss, and nutrient relations in contrasting environments, In: O. L. Lange, P. S. Nobel, C. B.Osmond and H. Ziegler (Eds.) pp 182-230. Encyclopedia of Plant Ecology 12B, Physiological Plant Ecology II, Springer, Berlin.
- [20]Kuppers, M., C. Giersch, H. Schneider and M. U. F. Kirschbaum. 1997. Leaf gas exchange in light- and sun-fecks: response patterns and simulations. In: H. Rennenberg, W. Eschrich and H. Ziegler (Eds.) pp 77–96. Trees contributions to modern tree physiology, Backhuys Publishers, Leiden, Netherlands.
- [21]Ladefoged, K. 1963. Transpiration of forest trees in closed stands. *Physiol. Plant.* 16:378–414.
- [22]Morecroft, M., H. Oliver, V. Stokes and J. Morison. 2000. Sensing and mis-sensing the eclipse. *Weather*. 55:174–176.
- [23]Haberle, K. H., I. Reiter, K. Patzner, C. Heyne and R. Matyssek. 2001. Switching the light off: A break in photosynthesis and sap flow of forest trees under total solar eclipse. *Meteorol. Z.* 10:201–206.
- [24] Jayaraman, J. 1981. Laboratory manual in biochemistry, Wiley Eastern Ltd, New Delhi.
- [25]Economou, G., E. D. Christou, A. Giannakourou, E. Gerasopoulos, D. Georgopoulos, V. Kotoulas, D. Lyra, N. Tsakalis, M. Tzortziou, P. Vahamidis, E.Papathanassiou and A. Karamanos. 2008, Eclipse effects on field crops and marine zooplankton: the 29 March 2006 total solar eclipse. *Atmos. Chem. Phys.* 8:4665–4676.
- [26]Gupta, U.S. 1994. Improving photosynthetic efficiency and crop productivity. In: S.S. Purohit and M.P Sahu (eds.) pp 1-50. Agro's Annual Review of Plant Physiology (Basic and Applied) Volume 1, Agro botanical Publishers (India), Bikaner, India.
- [27]Arora, D.K. and S. Gupta. 1996. Advances in Plant Physiology, Vol. 8, Anmol Publications Pvt. Ltd, New Delhi.
- [28]Danks, S. M., E. H. Evans and P. A. Whittaker. 1983. Structure function and assembly. In Photosynthetic systems, Wiley, New York.
- [29]Gamon, J. A. and J. S. Surfus. 1999. Assessing leaf pigment content and activity with a reflectometer. *New Phytol.* 143:105-117.

- [30]Young, A. and G. Britton. 1990. Carotenoids and stress. In Stress responses in plants: Adaptation and acclimation mechanisms, In: J. R. Cumming (Eds.) pp 87-112. Wiley-Liss, New York, USA.
- [31]Filella, I., L. Serrano, J. Serra and J. Penuelas. 1995. Evaluating wheat nitrogen status with canopy reflectance indices and discriminant analysis. *Crop Sci.* 35:1400-1405.
- [32]Schepers, J. S., T. M. Blackmer, W. W. Wilhelm and M. Resende. 1996. Transmittance and reflectance measurement of corn leaves from plants with different nitrogen and water supply. J. Plant Physiol. 148:523-529.
- [33]Kendrick R.E and G. H. Kronenberg. 1994. Photomorphogenesis in Plants. Martinus Nijhoff, Dordrecht, The Netherlands.
- [34]Baker N. R, and J. R. Bowyer. 1994. Photo inhibition of Photosynthesis. From Molecular Mechanisms to the Field. Bios Scientific Publishers, Oxford, UK.
- [35]Long S.P., S. Humphries and P.G. Falkowski. 1994. Photoinhibition of photosynthesis in nature. Ann. Rev. Pl.

Physiol. Pl. Mol. Biol. 45:633-662.

- [36]Herman E. and B.M. Sweeney. 1975. Circadian rhythm of chloroplast ultrastructure in Gonyaulax polyedra concentric organization around a central cluster of ribosomes. J. Ultrastr. Res. 50:347-354.
- [37]Vanden Driessche, T. 1966. Circadian rhythms in Acetabularia, photosynthetic capacity and chloroplast shape. *Exp. Cell Res.* 42:18-30.
- [38]Anderson, I. C. and I. S. Robertson. 1960. Role of carotenoids in protecting chlorophyll from photodestrtuction. *Plant Physiol.* 35:531-34.
- [39]Griffiths, M., W. V. R. Sistrom, G. Cohen-Bazire and R. Y. Stanier. 1955. Function of carotenoids in photosynthesis. *Nature*. 176:1211-214.
- [40]Aiitchell, R. L. and I. C. Anderson. 1965. Photoinactivation of catalase in carotenoidless tissues. Crop Sci. 5:588-91.
- [41]Seybold, A. and H. Falk, 1959. Die Heidelberger Chlorophyll bestimmungen-Eine Uberprufung. *Planta* 53:339-375.