Diurnal Cycle and Photoinhibition of Photosynthesis in Palm *Trachycarpus fortunei* H. Wendl. under Winter and Summer Conditions

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A study was conducted to analyze the contribution of high irradiance and resulting photoinhibition to the decline in net photosynthesis in the leaves of palm *Trachycarpus fortunei* during summer and winter as well as at normal growth and low temperatures in field and laboratory conditions, respectively. Fluorescence induction measurements indicated that there was a 10% decrease in the F_v/F_m ratio in field conditions at midday during both summer and winter, due to the relatively low intensity of incident light resulting from the partial leaf segment folding. Fluorescence parameters completely recovered by the evening hours. In summer the midday decay was due to the decrease of F_m which probably represents a rapidly reversible component of photoinhibition by the protective down-regulation of PSII mediated by the xanthophyll cycle. In winter, however, the initial F_v/F_m ratio was 40% less than as measured in summer and its midday decline was associated with the decrease of F_v indicating the partial inactivation of PS II. The net CO_2 assimilation rate followed the pattern of the F_v/F_m ratio but it could not recover due to the stomatal closure after midday. Comparing the fluorescence and gas exchange measurements we have concluded that the photoinhibition of *T. fortunei* represented by the F_v/F_m ratio changes is a regulatory adjustment of PS II efficiency to limiting carbon utilization and to limiting carbon availability imposed by stomatal closure. Leaves photoinhibited under laboratory conditions at growth temperature showed a substantial decrease of 50% in the F_v/F_m ratio due to the perpendicular exposure, but no apparent changes in D_1 protein content could be detected. Phytotron grown plants exposed to cold stress (6 °C) and low irradiance (250 μmol m^{-2} s^{-1}) under laboratory conditions showed a time related but much slower continuous decrease in F_v/F_m ratio. After high irradiance the recovery kinetics in the dark at normal growth temperature (28 °C) strongly depended on the extent of the photoinhibition, while after low irradiance complete recovery occurred in 12 hours irrespective of the initial F_v/F_m value, independently from the time of cold treatment, indicating that at low light and cold treatments only reversible inactive PS IIs were formed.

Introduction

Light is important to plants and to life on earth because it drives the process of photosynthesis. However, reduction in photosynthetic capacity called photoinhibition commonly occurs in nature when plants are exposed to solar radiation in excess of light energy necessary for photosynthetic or photorespiratory processes (Long *et al.,* 1994; Krause *et al.,* 1995). As the consequence of photoinhibition, midday decline of net CO_2 assimilation (A), stomatal conductance (S) as well as the decrease of maximum fluorescence (F_m) and that of the F_v/F_m ratio have been reported during the growing season for dicotyledon trees (Joshi, 1995; Pathre *et al.,* 1995; Krause *et al.,* 1995, Faria *et al.,* 1998), shrubs (Demmig-Adams *et al.,* 1989) and vines (Chaves *et al.,* 1987; Greer and Laing, 1992) of both tropical and temperate origins. Based on the recovery kinetics, it has been suggested that

Abbreviations and Symbols: A, net CO_2 assimilation; F_m, maximal level of fluorescence induction; F_o, initial part of fluorescence induction; F_v, variable part of fluorescence induction; PFD, photon flux density; PSII, photosystem 2; S, stomatal conductance; TL, thermoluminescence.

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the midday decrease in PSII efficiency involves at least two processes, one related to the xanthophyll cycle (Demmig-Adams and Adams, 1996), the other to the D_1 protein inactivation (Anderson *et al.,* 1997).

The inhibitory effect of cold stress together with high irradiance has also been reported on photosynthesis and related physiological processes for both cold tolerant and chilling sensitive plants (Huner *et al.,* 1993). For example, during winter and early spring evergreens such as conifers are subject to increased photoinhibition termed 'photochilling' in temperate climatic regions of the world (Bolhár-Nordenkampf and Lechner, 1988). Apparently the same is true in/from late autumn and/to early spring for a range of plants of subtropical origin like *Eucalyptus* (Ball *et al.,* 1991), sugar cane (Bolhár-Nordenkampf *et al.,* 1994) kiwifruit (Greer and Laing, 1992) grown under Mediterranean-type climates. Although, the key processes involved in the diurnal down regulation of photosynthesis have intensively been studied during the past decade, very little information is available on the high light induced alterations of physiological parameters in monocotyledon trees like the economically important palms, *Arecaceae* (Jayasekara and Jayasekara, 1995; Krause and Winter, 1996).

The Chinese windmill palm (*Trachycarpus fortunei*) used in our experiments is a characteristic landscape forming tree in South Europe, planted mainly in coastal towns, thus its significance in the tourism industry cannot be ruled out. It is one of the most frost tolerant species (Larcher *et al.,* 1991) of an otherwise tropical family (*Arecaceae*) of great economic importance. In some of its native and introduced habitats the species is subjected to low temperatures and is able to withstand temperatures down to −12 °C without any subsequent freeze damage (Larcher *et al.,* 1991).

In the present study therefore, we have attempted to make a comparative analysis on the contribution of high irradiance and cold stress to the operation of diurnal cycle of photosynthesis in palm *Trachycarpus fortunei* during summer and winter conditions, respectively. For a better understanding of the underlying mechanism we also carried out both *in vivo* and in *vitro* photoinhibition experiments under laboratory conditions.

Materials and Methods

Plant material

For the field experiments, measurements were made on the 3 youngest fully expanded leaves of five 10 year old, trunkless Chinese windmill palms, by other name Chusan palm (*Trachycarpus fortunei* Wendl) growing in the Arboretum of the University of Horticulture and Food Industry, Budapest. Measurements were made on three consecutive days in February and July 1997 and 1998 during longer periods of anticyclonal weather conditions. For the *in vivo* and *in vitro* measurements under laboratory conditions, greenhouse grown 6 month old seedlings were used. Five days prior to the exposure to *in vivo* photoinhibitory conditions the seedlings were transferred to growth cabinets (Weiss Technik Bioclim 1600SP), where the illumination followed 16 hrs light/ 8 hrs dark cycles, the photon flux density (PFD) was 250 μmol m^{-2} s^{-1} and the day/night temperature was constantly 28 °C.

Chloroplast isolation

Intact chloroplasts were isolated using the protocol of Horváth *et al.* (1983).

Photoinhibition and recovery under laboratory conditions

Leaves were placed horizontally on wet filter paper. *In vivo* photoinhibition was induced by two 500-W metal-halide lamps with a photon flux density of 1.6–1.7 mmol m^{-2} s^{-1} upon exposure on the adaxial side of the leaves. Air temperature was kept at 6 °C in a cold room or 28 °C by placing a cold water bath between the light source and the leaves. For the recovery from photoinhibition, the plants were placed in complete darkness at a temperature of 25 °C. For *in vitro* photoinhibition, 1 ml of chloroplast suspension isolated from greenhouse grown leaves were placed in glass cuvettes with 1 mm thickness under the above conditions and illuminated for 5, 10, 20, 30 and 60 min.

Chlorophyll fluorescence

Chlorophyll fluorescence was recorded in both field and laboratory conditions with a portable fluorometer (Plant Efficiency Analyser, Hansatech Ltd., King's Lynn, U. K.). After 15 minutes of dark

adaptation samples were excited with the actinic PFD of 1800 μmol m^{-2} s^{-1} at 650 nm. Fluorescence was detected for 120 sec and the usually used parameters: F_o, F_v, F_m and the F_v/F_m ratio were calculated (Bolhár-Nordenkampf and Öquist, 1993).

Photosynthetic gas exchange

The net photosynthesis of field grown palm leaves were measured in every second hour of sunlight days by LI-COR (LI-6200, USA) portable gas exchange system according to Winner *et al.* (1989). Total sunlight leaf parts were closed into a chamber of 250 cm^3 with an area of 20–25 cm^2. The net photosynthesis values were calculated by the system and the average of six independent measurements were used.

Stomatal conductivity

Stomatal conductance was measured with a portable mass flow porometer (AP4 Delta-T Devices, Cambridge, U. K.) according to Tuba *et al.* (1998).

Measurement of thermoluminescence

The TL of leaf discs with a 10 mm diameter or 0.5 ml chloroplast suspension containing 125 μg chl were measured using an apparatus similar to that described earlier (Demeter *et al.*, 1979). The light source was a 650 W tungsten lamp provided 10 W m^{-2} irradiance on the surface of the sample. Samples were illuminated at the specified temperature and rapidly cooled down to −80 °C. TL was measured during heating the sample in darkness with a constant heating rate of 20 °C min^{-1}.

Immunological detection of the D_1 protein

The analysis was made on both *in vivo* and *in vitro* photoinhibited samples based on the work of Blake *et al.* (1984) and modified by Georgakopoulos and Argyroudi-Akoyunoglou (1997).

Results and Discussion

Photoinhibition under field conditions

Plants subject to high irradiance at normal growth and low temperatures exhibit different photoinhibitory responses which are resulted by various concomitant and subsequent molecular

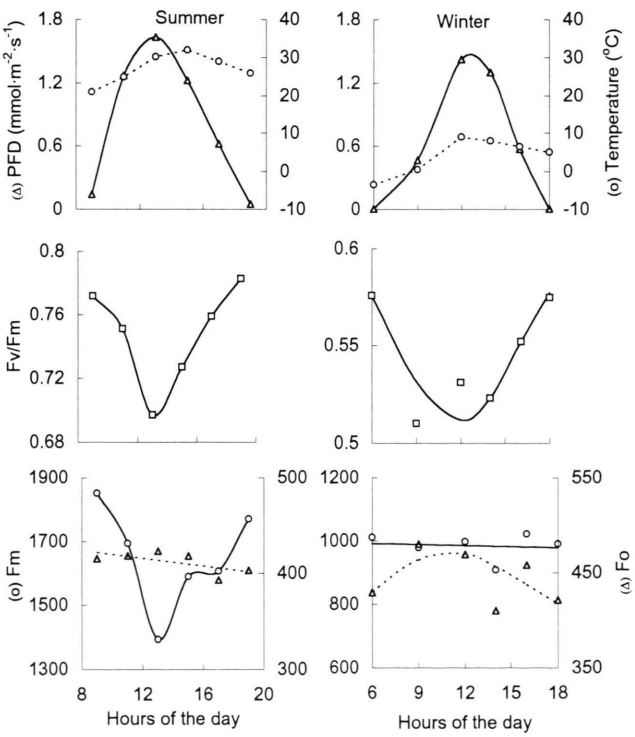

Fig. 1. Diurnal changes of the fluorescence induction characteristics of field grown *T. fortunei* leaves exposed by high light during summer and winter periods. Top panels represent the typical changes of light intensity and temperature during one day of the measurements.

events (for reviews see Long *et al.* 1994; Huner *et al.* 1993; Krause 1994 and references therein). In order to obtain information about the photoinhibitory response of palm, *T. fortunei*, the diurnal fluctuations of the fluorescence induction characteristics were compared in summer and in winter, respectively. As shown in Fig. 1 (top panels), in both cases the maximal light intensities were similar (1.7 and 1.5 mmol $m^{-2} s^{-1}$). The daily temperature regime in summer (25–32 °C) corresponded to the normal growth temperature, while in winter measurements plants were subjected to chilling or freezing temperatures (–3,2 to 5 °C). In both summer and winter, fluorescence measurements made under field conditions showed similar, only approximately a 10% decrease in the PSII activity as indicated by the change of the F_v/F_m ratio (Fig. 1 middle panels). The inhibition was completely reversible and was fully recovered by the evening hours. In summer, the decrease in the F_v/F_m ratio was due to the decrease of F_m since F_o was practically unaltered during the day (Fig. 1 lower panels) which might be the result of the increase in xanthophyll cycle dependent energy dissipation in the antennae (Demmig-Adams and Adams, 1996; Jahn and Miehe, 1996). In winter, however, the F_v/F_m ratio was markedly lower than in summertime (Fig. 1. middle panels), which fitted well to earlier results obtained by the seasonal variation of the F_v/F_m (Bolhár-Nordenkampf and Lechner, 1988; Ottander *et al.*, 1995) and explained by low temperature induced partial inactivation of PS II activity (Huner *et al.*, 1993). The diurnal alteration of the F_v/F_m ratio was due to the changes in F_v (significant increase of F_o at midday with an unchanged F_m) which indicated that parallel with the energy dissipation mechanism, PS II inactivation also occurred (Krause, 1994; Schettger *et al.*, 1994; Krause, 1988).

Since, according to the definition of Long *et al.* (1994) "light impairment of PS II is only photoinhibition if a decrease in the overall photosynthetic rate results ", we measured the diurnal fluctuation of the net CO_2 assimilation in the field at normal growth conditions. As shown in Fig. 2.A the net CO_2 assimilation after a slight increase had the minimum value at similar midday hour as the F_v/F_m ratio but it could not return to the original value, just exhibited a second but much lower peak during the afternoon hours. Similar double peak diurnal curves were reported by Pathre *et al.* (1995) for different tree species.

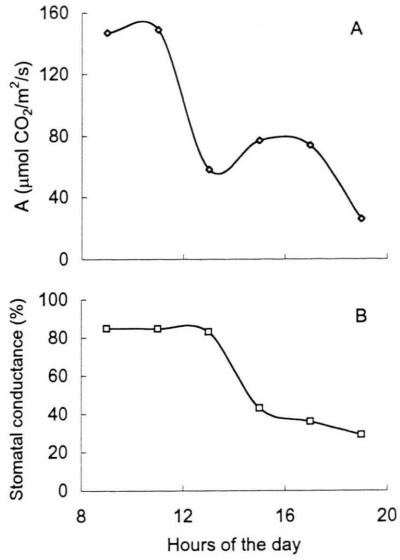

Fig. 2. Daily alterations of the net CO_2 fixation (A) and stomatal conductance (B) of field grown *T. fortunei* leaves exposed to high light during summer.

Chaves *et al.* (1987) demonstrated a strong correlation between net photosynthesis and stomatal conductance in grapevine cultivars. In our case, however, the stomatal closure was not correlated with the net CO_2 assimilation, because it declined only at midday when the CO_2 gas exchange reached its minimum value and remained low during the rest of the day (Fig. 2.B). The high stomatal conductance in the morning hours indicates that the decrease in the net CO_2 fixation is the result of the intrinsic changes in the CO_2 fixation rather than the CO_2 limitation modulated by stomatal closure. The low net CO_2 gas exchange in the afternoon hours is well explained by the stomatal closure (Chaves *et al.*, 1987). Comparing the data of fluorescence induction measurements and the CO_2 gas exchange, we have concluded that the photoinhibition of *T. fortunei* under field conditions measured by the F_v/F_m ratio is a regulatory adjustment of PS II efficiency to limiting carbon utilization and to limiting carbon availability imposed by stomatal closure (Demmig-Adams and Adams, 1996; Faria *et al.*, 1998).

Photoinhibition under laboratory conditions

After 120 min photoinhibition of 6 month old intact palm leaves induced at 28 °C under laboratory conditions, a 50% decrease was observed in the F_v/F_m ratio and more than 40% rise in the F_o value (Fig. 3). At low temperature (6 °C) similar changes were observed with a maximum deviation of 10% (data not shown). The decrease in the F_v/F_m ratio could not be the result of the limited carbon availability modulated by stomatal closure because stomatal conductance was increased due to the high water pressure during the experiment. The dramatic decrease in the TL intensity during photoinhibition indicated a substantial damage in PS II

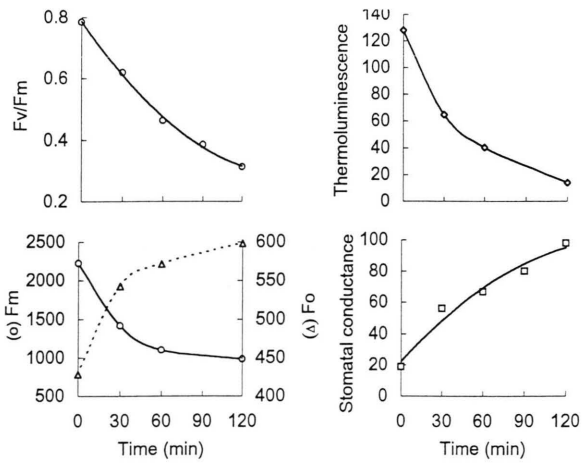

Fig. 3. Changes of fluorescence induction characteristics, thermoluminescence and stomatal conductivity of *in vivo* photoinhibited *T. fortunei* leaves under laboratory conditions. Light intensity, 1.6–1.7 mmol m^{-2} s^{-1}, temperature, 28 °C.

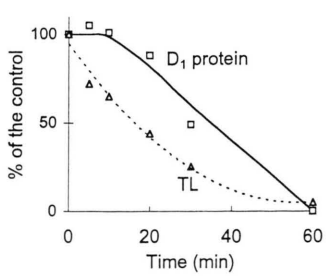

Fig. 4. Decrease of thermoluminescence intensity and the D_1 protein content of isolated *T. fortunei* chloroplasts during photoinhibition. Light intensity 1.6–1.7 mmol m^{-2} s^{-1}, temperature 28 °C, chlorophyll concentration: 1 mg/ml, thickness of the chloroplast layer: 1 mm.

function which was not associated with any D_1 degradation (data not shown). This is in agreement with the earlier observation that *in vivo* photoinhibition caused loss of photochemical activity without the degradation of D_1 polypeptide (Cleland *et al.*, 1990). Isolated *T. fortunei* chloroplasts under similar photoinhibitory conditions, however, completely lost the PS II activity with a concomitant D_1 protein degradation (Fig. 4). The fact that PS II inactivation partially preceeds the loss of D_1 protein is in accordance with the general view that the impairment of PS II electron transport triggers the D_1 degradation (for review see Andersson, 1992; Anderson *et al.*, 1997; Long *et al.*, 1994 and references therein). The difference between the *in vivo* and *in vitro* photoinhibition can be explained in the following way: *In vivo* mainly reversibly inactivated PS II are formed (Long *et al.*, 1994) while *in vitro* the high O_2 concentration of the suspension buffer enhances the formulation of the highly toxic oxygen radical ($^1O_2$) resulting in a complete irreversible inhibition and/or destruction of PS II (Vass and Styring, 1993; Hideg *et al.*, 1994).

This assumption seems to be verified by the recovery experiment (Fig. 5). The decreased F_v/F_m ratio of photoinhibited leaves could be restored in the dark but the rate of recovery was strongly dependent on the extent of photoinhibition. 20% decrease of the F_v/F_m ratio was practically recovered after 24 hours, while at 60% photoinhibition the F_v/F_m ratio was restored only in 70% even after 96 hours of dark recovery. *In vitro* no recovery could be found at any degree of photoinhibition (data not shown). Leaves subjected to low light (250 μmol m^{-2} s^{-1}) at low (6 °C) temperature also showed a stepwise decrease in the F_v/F_m ratio but the rate of decrease was smaller by order of magnitude (Fig. 5. C). The F_v/F_m ratio was recovered in the dark within 12 hours independently from the extent of the F_v/F_m reduction similarly to the results of Janda *et al.*, (1994). Our result is consistent with the earlier finding that at low light and low temperature conditions only reversibly inactivated PS II were formed (Briantis *et al.*, 1992) and this form could not be converted to non-reversible inactive PS II centers (Long *et al.*, 1994).

Comparing the different data obtained in field and laboratory conditions the difference between the results can be explained on the following way:

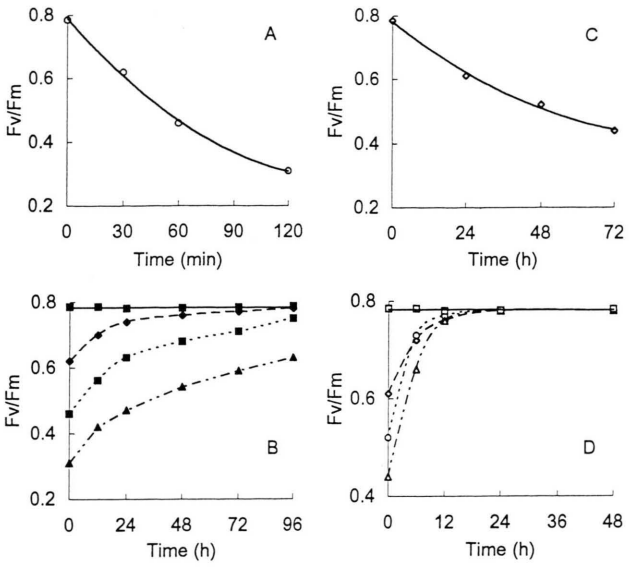

Fig. 5. *In vivo* changes of the F_v/F_m ratio (A, C) and its dark recovery kinetics (B, D) of *T. fortunei* leaves treated with high light (1.6–1.7 mmol m^{-2} s^{-1}) at normal growth temperature of 28 °C (A, B) or treated with low light intensity (250 μmol m^{-2} s^{-1}) at low temperature of 6 °C (C, D).

younger leaves are more sensitive to photoinhibition than mature leaves (Krause *et al.*, 1995). Under field conditions mature leaves have a venation, a V fold of the leaf segments, thus irradiance reaches the leaves at different angles resulting in a significant decrease of the intensity of incident light. Whereas under laboratory conditions juvenile leaves of the seedlings lack the typical V-fold and high irradiance reached the leaves perpendicularly. Leaves in the field showed a further slight folding of the segments during the noon hours perhaps as a means of high irradiance avoidance which was also observed in other plants (Ludlow and Björkman, 1984).

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