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Diurnal and seasonal changes in photosynthesis and photosystem 2 photochemical efficiency in *Prosopis juliflora* leaves subjected to natural environmental stress

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Abstract

The plants of *Prosopis juliflora* growing in northern India are exposed to large variations of temperature, vapour pressure deficits (VPD), and photosynthetic photon flux density (PPFD) throughout the year. Under these conditions *P. juliflora* had two short periods of leaf production, one after the winter season and second after summer, which resulted in two distinct even aged cohorts of leaves. In winter with cold nights (2-8 °C) and moderate temperatures during the day, the plants showed high rates of photosynthesis. In summer the midday temperatures often reached <45 °C and plants showed severe inhibition of photosynthesis. The leaves of second cohort appeared in July and showed typical midday depression of photosynthesis. An analysis of diurnal partitioning of the absorbed excitation energy into photochemistry showed that a smaller fraction of the energy was utilised for photochemistry and a greater fraction was dissipated thermally. further the photon utilisation for photochemistry and thermal dissipation is largely affected by the interaction of irradiance and temperature. The plants showed high photochemical efficiency of photosystem 2 (PS2) at predawn and very little photoinhibition in all seasons except in summer. The photoinhibition in summer was pronounced with very poor recovery during night. Since *P. juliflora* exhibited distinct pattern of senescence and production of new leaves after winter and summer stress period, it appeared that the ontogenic characteristic together with its ability for safe dissipation of excess radiant energy in *P. juliflora* contributes to its growth and survival.

Additional key words: chlorophyll fluorescence; diurnal courses; electron transport rate; irradiance; midday depression; non-photochemical quenching; photoinhibition; photosystem 2; temperature.

Introduction

Prosopis juliflora is a semi-deciduous species characterised with peculiar phenology of multiple growth periods during one year resulting in concurrent leaf cohorts (Sharifi *et al.* 1983, Nilsen *et al.* 1986). This species is known for its hardy nature, multiple uses, and nitrogen fixing ability. It grows profusely and forms a dominant woody element over large areas of the world, particularly on infertile soils, deserts, and semiarid communities (Goel and Behl 2000). In India this species is of great value for reclamation of saline and alkaline soils, especially in the northern parts of the country (Goel and Behl 1995, 2001). The environmental conditions in north India are typically tropical, with distinct hot summer season (April-June) and distinct winter season (November-January). The summer season is characterised by temperature extremes of around 45 °C and VPD exceeding 8.0 kPa. In winter, in contrast the day temperatures are moderate and the night temperatures often dip to less than 5 °C. Under these environmental conditions *P. juliflora* sheds its leaves twice, once during February-March and next in July-August. Unlike typical deciduous plants the shedding of leaves is accompanied with the formation of new leaves. The periods of senescence and growth of new leaves are very short and thus plants appear evergreen.

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Abbreviations: D, proportion of absorbed radiant energy dissipated as heat; E, excess, proportion of absorbed radiant energy which is neither dissipated nor used in photochemistry; ETR, apparent electron transport rates; F_0 minimal fluorescence of a dark-adapted leaf; F_0', minimal fluorescence of a light-adapted leaf; F_m, maximum fluorescence of a dark-adapted leaf; F_m', maximum fluorescence of a light-adapted leaf; F_v/F_m, maximal photochemical efficiency of PS2 in a dark-adapted leaf; F_v'/F_m', photochemical efficiency of PS2 in a light-adapted leaf; $\Delta F/F_m'$, overall photochemical quantum yield of PS2; HDR, heat dissipation rate; NPQ, non-photochemical fluorescence quenching; P, proportion of absorbed radiant energy used in photochemistry; P_N, net photosynthetic rate; PPFD, photosynthetic photon flux density; PS2, photosystem 2; VPD, leaf to air vapour pressure deficit.

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The ontogenic behaviour of *Prosopis* leaves may contribute to the high adaptability of this species, since only mature leaves of *P. juliflora* are exposed to stress periods of winter and summer, while young leaves always grow in optimal environment.

In addition to temperature stress the plants are exposed to high irradiance throughout the year in this part of the subcontinent. In order to tolerate high excitation pressure, the successful species like *P. juliflora* should have an efficient mechanism of dissipation of excess photons. A number of physiological processes have been described which help to balance photon absorption and utilisation of electronic excitation in the continuously changing natural environment (Niyogi 1999). Among them, the radiation-less energy dissipation as heat plays a major role in photoprotection and is one of the most extensively studied processes (Adams and Demmig-Adams 1995, Verhoeven *et al.* 1998). However, under tropical environments these mechanisms could be further complicated by the interactions of multiple environmental factors, such as temperature and VPD (Kitao *et al.* 2000). Gas exchange measurements have shown that the maximum photosynthesis rate of *P. juliflora* varies significantly in different seasons, although the diurnal pattern of PPFD is almost constant in different seasons (Pathre *et al.* 1998, Shirke 2002). The variations in photosynthesis rate could be due to altered photon dissipation capacity in different cohorts of leaves in different seasons or due to the interaction of radiation with temperature and VPD, affecting the excess photon dissipation and causing photoinhibition. In the present paper, we studied the photosynthetic responses and partitioning of the absorbed photon energy into photochemistry *versus* thermal dissipation of *P. juliflora* leaves, to the changing environment in different seasons from spring to winter. Measurements were made monthly from February till December. The leaves of *P. juliflora* are well suited for this type of study as they grow in distinct, clearly defined, and seasonally unchanged orientations. Secondly, the continuous assessment (both diurnal and seasonal) of the same plants (and leaves wherever possible) clearly revealed the interactive effect of environmental changes.

Materials and methods

Plants: Two-year old plants of *Prosopis juliflora* (Sw.) DC., growing in 10 000 cm^3 plastic pots on the terrace garden of the Institute under natural conditions throughout the year, were used for all experiments. The plants were watered everyday and were supplied with Hoagland's solution fortnightly. Measurements were carried out on fully developed mature leaves. The study was divided into four seasons, and the months which represent the seasons are March (spring), May and June (summer), July and September (monsoon), and December (winter). All the measurements were made on clear sunny days from pre-dawn till dusk.

Measurement of photosynthetic parameters: Net photosynthetic rate (P_N) and the environmental parameters, *i.e.* photosynthetic photon flux density (PPFD), air temperature (T), and vapour pressure deficit (VPD), were measured using *Li-Cor* model *6200* portable photosynthesis system attached with 1 000 cm^3 chamber (*Li-Cor*, NE, USA). The leaf used for study was fully exposed and oriented to normal irradiation during measurements to ensure the measurements of gas exchange at the highest possible PPFD.

Chlorophyll fluorescence measurements: Diurnal changes in chlorophyll fluorescence parameters were monitored under field conditions using portable pulse amplitude modulation flurometer (*PAM-2000*) and the *2030-B* leaf-clip holder (*H. Walz*, Effeltrich, Germany). The leaf-clip holder allows the simultaneous recording of the PPFD incident on the leaf and abaxial leaf temperature (T_l).

Minimal and the maximal fluorescence yield of a dark-adapted leaf, F_0 and F_m, respectively, were measured at pre-dawn or after sunset. For the calculation of PS2 maximum photochemical efficiency the predawn values of F_0 and F_m were used [$F_v/F_m = (F_m - F_0)/F_m$]. The actual photochemical efficiency of PS2 under irradiation was calculated according to Genty *et al.* (1989) as $\Delta F/F_m' = (F_m' - F_s)/F_m'$. The value of $\Delta F/F_m'$ was integrated over the entire day (P) to get the proportion of absorbed radiant energy used in PS2 photochemistry, the fraction of absorbed photons that is dissipated thermally (D) was estimated as $1 - F_v'/F_m'$ (Demmig-Adams *et al.* 1996). The proportion of absorbed radiant energy used neither in photochemistry nor dissipated was assumed to be in excess as $E = F_v'/F_m'\ (1 - q_p)$. The actual photochemical efficiency of PS2 under irradiation was further used to calculate the rate of photochemistry or the apparent electron transport rate (ETR) as ETR = $\Delta F/F_m'$ PPFD. The heat dissipation rate, HDR, was calculated in a similar way as ETR, but with $1 - F_v'/F_m'$ instead of $\Delta F/F_m'$ (Demmig-Adams *et al.* 1996). The energy dissipation activity was estimated from the non-photochemical fluorescence quenching (NPQ) of F_m' as $(F_m - F_m')/F_m'$ (Bilger and Björkman 1990).

At least 10 measurements were made on different leaves of each plant. The results shown are means ± SD of the measurements made on four different plants.

Results and discussion

Table 1 summarises the performance of *P. juliflora* leaves produced in two-growth periods. The values show the predawn and sunset measurements of initial fluorescence (F_0), maximal fluorescence (F_m), and the ratio of variable and maximum fluorescence (F_v/F_m) in different months. The new leaves in March and July showed F_m values greater than 2.0 with F_v/F_m value around 0.8. The values of F_v/F_m of a dark-adapted leaf reflect the potential quantum efficiency of PS2 and are used as a sensitive indicator of plant photosynthetic performance. The optimal value of around 0.80 for F_v/F_m ratio was found for most plant species (Krause *et al.* 1995, Zhang and Gao 1999, Kitao *et al.* 2000, Shirke 2001, Oliveira and Peñuelas 2002). We measured the F_v/F_m at predawn and after sunset only and not during the day, as the measurement of F_m requires darkening of the leaves for considerable period, which could have affected the normal diurnal cycle under field conditions. Nevertheless, the predawn and sunset values should indicate the extent of recovery from photoinhibition (Krause *et al.* 1995, Zhang and Gao 1999, Shirke 2001). The values for March and July represented the unstressed conditions of leaves. In May and September, the performance of *Prosopis* leaves was slightly affected mainly due to the change in temperatures during the day, as the PPFD remained fairly constant (Figs. 1 and 2). Table 1 shows lowest values of F_0, F_m, and F_v/F_m in December and June that represent the stress periods of winter and summer seasons, respectively. F_m is sensitive to the prehistory of the plant (Gamon and Pearcy 1990) and hence the lower value of F_m indicates the persistence of diurnal environmental stress. The low values of F_v/F_m at predawn in winter and summer showed sustained photoinhibition, low night temperatures could have probably prevented the complete nocturnal recovery of F_v/F_m values in winter (Verhoeven *et al.* 1999) and thus F_v/F_m ratio showed the long-term stress effects on the leaves. The lower predawn values of F_v/F_m in winter and summer indicates the interactive effects of irradiation and temperature since the plants were exposed to similar irradiances in spring and monsoon seasons, but the night recoveries of F_m and F_0 were likely possible only at moderate temperatures. We did not observe much change between the predawn and the sunset values of F_m and F_v/F_m for a given month, suggesting that the fast relaxation of photoinhibition occurred already during irradiation period (Krause *et al.* 1995). Thus the seasonal changes could be the result of gradual accumulation of stress effects.

Table 1. Changes in minimal (F_0) and maximum (F_m) fluorescence, and maximum photochemical efficiency of PS2 (F_v/F_m) of a dark-adapted leaf and leaf temperature (T_l) in *P. juliflora* leaves measured in different seasons. Values in parenthesis are the means ± SE from measurements of four independent plants.

Date	Predawn				Sunset			
	F_0	F_m	F_v/F_m	T_l	F_0	F_m	F_v/F_m	T_l
13 March	0.44 ± 0.02	2.26 ± 0.12	0.79 ± 0.01	24.0 ± 0.4	0.44 ± 0.03	2.11 ± 0.04	0.79 ± 0.02	29.0 ± 0.2
20 May	0.35 ± 0.02	1.77 ± 0.15	0.77 ± 0.01	26.0 ± 0.2	0.41 ± 0.01	1.89 ± 0.05	0.78 ± 0.01	35.0 ± 3.0
1 June	0.21 ± 0.01	1.07 ± 0.04	0.61 ± 0.02	30.0 ± 0.3	0.22 ± 0.01	1.00 ± 0.03	0.51 ± 0.02	39.0 ± 0.1
23 July	0.41 ± 0.04	2.05 ± 0.18	0.80 ± 0.01	29.0 ± 0.2	0.40 ± 0.02	2.08 ± 0.20	0.77 ± 0.01	30.5 ± 0.3
30 September	0.40 ± 0.01	1.99 ± 0.12	0.80 ± 0.02	23.5 ± 0.2	0.40 ± 0.02	1.87 ± 0.06	0.78 ± 0.01	32.0 ± 0.1
22 December	0.36 ± 0.01	1.69 ± 0.05	0.79 ± 0.01	15.0 ± 0.5	0.34 ± 0.01	1.57 ± 0.01	0.76 ± 0.01	22.0 ± 0.3

To analyse the changes in photosynthesis and the actual quantum efficiency of PS2 in response to diurnal environmental cycle, the set of measurements was made along with environmental variables for each cohort of leaves of *P. juliflora* in different seasons. During spring season *P. juliflora* produced its first cohort of leaves. In March the temperature ranged from 22 to 30 °C while PPFD showed typical bell shaped curve with maximum around 2 000 µmol m^{-2} s^{-1} during midday. P_N increased sharply, parallel to the PPFD, and reached a maximum of around 16 µmol m^{-2} s^{-1} at 10:00 (Fig. 1). The rate slightly decreased thereafter till 15:00 and declined sharply with further decline in PPFD. The summer in north India is characterised with high temperatures and VPD. In May the temperatures increased continuously till midday and reached more than 40 °C, subsequently VPD also rose sharply and reached around 8.5 kPa during midday. The high temperature and high VPD affected the overall photosynthesis severely. The summer stress was further augmented in June with temperatures exceeding 45 °C during noon. The maximum P_N of around 10 µmol m^{-2} s^{-1}, which was confined to early morning period, decreased continuously till it reached almost zero by 14:00. The severe inhibition in photosynthesis observed in June could have resulted from the cumulative effect of increasing stress over the period of two months.

In the beginning of monsoon, the second cohorts of leaves were produced. The measurements made on the fully developed leaves from second growth period are depicted in Fig. 2. In the second cohort of leaves of *P. juliflora* showed a bimodal diurnal pattern of photosynthesis with a depression of photosynthesis around noon. The rains brought down the maximum temperature to around 40 °C, and VPD to less than 6.0 kPa, which was 30 % less than that observed in June. In September the temperatures were further decreased, but PPFD remained high. There was no significant difference in the P_N pattern except the overall P_N in September was higher than that of July with better recovery of photosynthesis after midday depression. In winter the night temperatures were low (≈5 °C, values not shown) but the maximum temperatures during the day exceeded 30 °C, and the PPFD remained high during the day. In winter the bimodal curve of photosynthesis disappeared, and bell-shaped curve, parallel to PPFD, was observed (Fig. 2). P_N increased gradually with increase in the PPFD and temperature and reached its maximum at midday, and later decreased gradually.

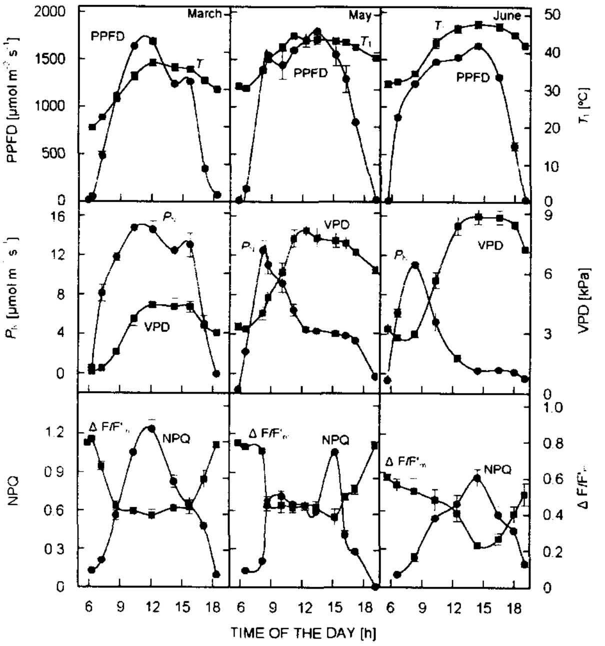

Fig. 1. Diurnal changes in net photosynthetic rate (P_N), photochemical efficiency of photosystem 2 (ΔF/F$_m$'), and non-photochemical quenching (NPQ) in first cohort of leaves of *P. juliflora*, along with the changes in environmental parameters, viz. incident photosynthetic photon flux density (PPFD), leaf temperature (T_l), and vapour pressure deficit (VPD). The values for different months represent different seasons, March (spring), and May and June (summer). Each point (bar) represents the mean ± SE from measurements of four independent plants at each diurnal hour.

Energy utilisation by a leaf is reflected by the diurnal changes in ΔF/F$_m$' which measures the proportion of the photons absorbed by chlorophyll associated with PS2 that is used in photochemistry and thus indicates overall photosynthesis (Genty *et al.* 1989). The diurnal pattern of ΔF/F$_m$' observed in *P. juliflora* was high (around 0.8) at sunrise in all the seasons except in late summer (June) and then decreased with increase in the PPFD, and reached a minimum (Figs. 1 and 2). In the afternoon ΔF/F$_m$' showed increasing trend with decreasing PPFD and reached the predawn value in the evening. The overall trend for diurnal course of ΔF/F$_m$' is similar in all seasons, which is primarily due to similar pattern of PPFD experienced by *Prosopis* plants. However, the shape of the diurnal curve for ΔF/F$_m$' showed remarkable differences apparently due to the interactions of irradiance and other environmental parameters such as temperature and VPD. The effects of these interactions were clearly visible in June. The diurnal curve of ΔF/F$_m$' in June showed low value (0.6) prior to sunrise, which decreased continuously till midday. After midday the ΔF/F$_m$' further dropped sharply to 0.25 and then recovered partially in the evening. The midday decline observed in June reflects the interactive effects of irradiance and temperature along with the VPD. Pathre *et al.* (1998) showed that the high VPD could severely affect the photosynthesis and stomatal conductance in *P. juliflora* under field conditions as well as under controlled conditions. Furthermore, restricted CO_2 availability could also lead to increased susceptibility of photodamage (Franco and Lüttge 2002). In the second cohorts of leaves of *P. juliflora* the pattern of ΔF/F$_m$' appeared to be similar in different seasons including winter probably due to moderate environmental

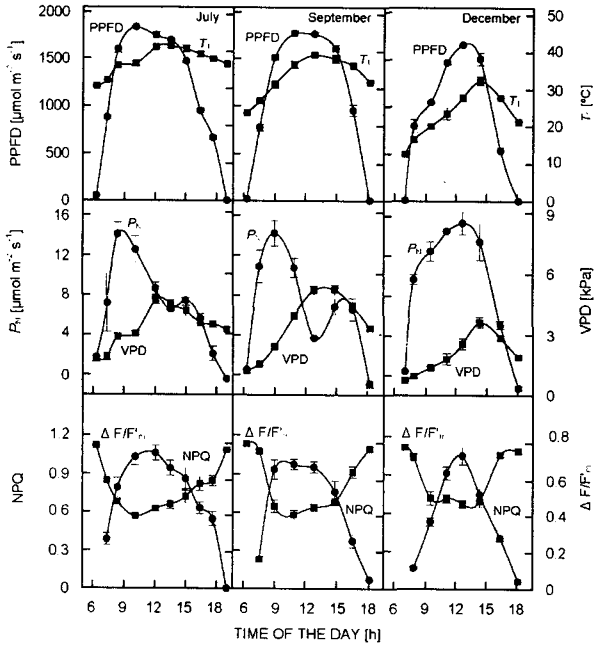

Fig. 2. Diurnal changes in net photosynthesis rate (P_N), photochemical efficiency of PS2 (ΔF/F$_m$'), and non-photochemical quenching (NPQ) in second cohort of leaves of *P. juliflora*, along with the changes in environmental parameters viz. incident photosynthetic photon flux density (PPFD), leaf temperature (T_l), and vapour pressure deficit (VPD). The data are shown for different months representing different seasons, July, September (monsoon), and December (winter). Each point (bar) represents the mean ± SE from measurements of four independent plants at each diurnal hour.

conditions during the day. In December the $\Delta F/F_m'$ was not affected by the low night temperatures (Fig. 2). The continuous measurements on two types of leaves showed that ageing does not affect the photochemical PS2 efficiency, since a similar diurnal pattern was observed for young and old leaves.

The decrease in $\Delta F/F_m'$ observed in *P. juliflora* leaves during diurnal cycle may be due to the decrease in F_m' rather than the changes in F_0' (Fig. 3). The changes in F_m' reveal distinct, interactive effects of sunlight and temperature on PS2 (Gamon and Pearcy 1990). In March the new and mature leaves showed the typical parabolic pattern of sun leaves with high F_m' (2.0) in the morning, decreased gradually, reached minimum (1.0) during midday, and then gradually increased in the afternoon (Fig. 3). In summer, a similar diurnal trend was observed for F_m' but the decline was much steeper and showed minimal value for most of the day period. In June low value of F_m' was observed in early morning (1.0), which decreased further (0.3 at 15:00) during the course of the day. In the evening, F_m' recovered back to 0.9 (Fig. 3). The new leaves in July showed high F_m' in the morning, then decreased gradually during midday, and then again recovered completely in the evening (Fig. 3). In winter, F_m' (Fig. 3) was somewhat low in the morning (1.6), probably due to the low temperatures (Greer and Laing 1988).

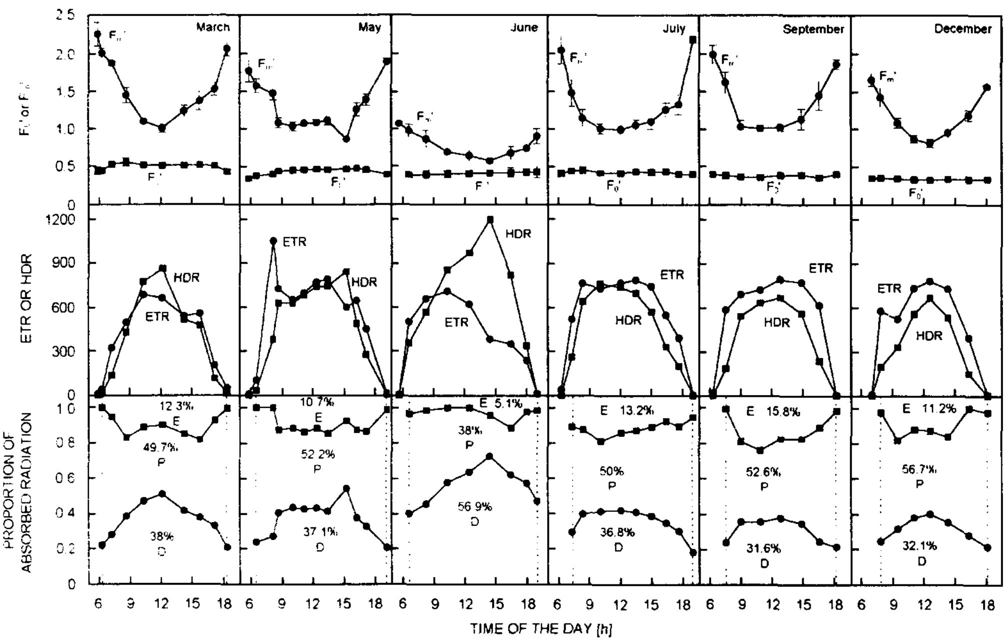

Fig. 3. Diurnal changes in the initial fluorescence (F_0') and maximum fluorescence (F_m') in light, estimated rates of apparent electron transport (ETR) and heat dissipation rate (HDR), the allocation of absorbed radiant energy into fractions used in photochemistry (P), dissipation (D), or excess (E) in the first cohort of leaves of *P. juliflora* in different seasons, March (spring), May and June (summer), July and September (monsoon), and December (winter). Each point (bar) represents the mean ± SE, from measurements of four independent plants at each diurnal hour.

The decline observed in F_m' during the day and its recovery in the evening may be an expression of the onset of protective mechanisms allowing an improved thermal de-excitation of PS2 (Valentini *et al.* 1995) and measured as NPQ (non-photochemical quenching). Diurnal measurements of NPQ (Figs. 1 and 2) showed the fraction of absorbed energy dissipated thermally was low prior to sunrise, rose during exposure to direct sunlight reaching a maximum concomitant with maximal incident sunlight, and decreased to predawn values by the end of the day. However, the NPQ curves showed marked differences in each month. In March the new leaves of first cohort of *Prosopis* showed highest value of 1.3 for NPQ at midday (Fig. 1), while the new leaves of second cohort appearing in July showed NPQ less than 1.0 at noon (Fig. 2). In May the NPQ showed two peaks one around 10:00 and second sharp peak appeared at 15:00. In June the first peak disappeared and only one peak (<0.9) appeared at around 14:00 (Fig. 1).

The seasonal trend for radiant energy utilisation could be evaluated from the relative rates of photochemistry (ETR) and thermal dissipation (HDR). The diurnal curves of ETR and HDR were similar and parallel to the curves for PPFD in different seasons (Fig. 3) and apparently did not show limitations under seasonal changes, however, the area under the curve decreased as seasons proceeded from monsoon to winter. The similar pattern of ETR and HDR in different seasons showed the adjustments in the partitioning of electron flow between assimilative and non-assimilative processes were enough to maintain high electron flow, even though CO_2 assimilation showed large variations. We also observed that though increased temperatures favoured the ETR, the extreme temperatures in summer might have detrimental effect on ETR, as observed in June. In June *Prosopis* leaves showed decline in ETR after 10:00 (Fig. 3) when temperature exceeds 45 °C (Fig. 1). In different seasons the estimated rates of photochemistry were slightly higher than that of thermal dissipation, except in June. In June the rate of thermal dissipation (HDR) was considerably higher than that of the rate of photochemistry (ETR) (Fig. 3).

The proportion of the absorbed photons, integrated over the whole day showed that in June almost 60 % of the radiant energy was dissipated while in other months it was in the rage of 32-38 % (Fig. 3). Similarly the excess fraction (E) was always in the range of 10-15 % during the year except in June (5 %). Since the E values are generally overestimated at the expense of P under high irradiance (Demmig-Adams *et al.* 1996, Oliveira and Peñuelas 2001), the lowest value of E in June further substantiated the data on large thermal dissipation of absorbed photons. The new leaves of different growth period showed almost similar rates for photochemistry and heat dissipation indicating that there was no difference in the inherent capacity of photon utilisation for photochemistry or for thermal dissipation. Therefore the large increase in thermal dissipation may have resulted from the interaction of radiant energy with high temperature and high VPD.

The mechanism of photoinhibition and relaxation kinetics by xanthophyll cycle-dependent energy dissipation suggests two forms: one, which relaxes rapidly with the lowering of irradiance or temperature stress, and another, which relaxes slowly (Krause *et al.* 1995). In *Prosopis,* though sustained photoinhibition occurred during summer and winter, the new leaves were formed in subsequent months and therefore the recovery from sustained inhibition was probably not needed. Most of decline in photochemical efficiency was related to the fast-relaxing component of non-photochemical quenching as evidenced by high values of F_v/F_m at predawn in all the seasons except in summer and winter, secondly the complete recovery in F_v/F_m was observed at sunset. This component likely corresponds to energy dissipation *via* build-up of an electrochemical gradient across the thylakoid membranes and de-epoxidation of violaxanthin to zeaxanthin (Krause *et al.* 1995, Adams and Barker 1998). Thus this decrease in photochemical efficiency maintains the balance between light-driven linear flow of electrons and requirement of reducing equivalents, for both carboxylation and oxygenation of RuBP (Krause and Weis 1991, Valentini *et al.* 1995). Persistent reductions in PS2 efficiency under low/high temperature and high irradiance are attributed predominantly to the retention of de-epoxidised components of the xanthophyll cycle and their sustained engagement for energy dissipation activity (Gilmore 1997, Havaux *et al.* 2000). The sustained reduction of F_v/F_m in winter and summer may also result from accumulation of non-functional PS2 reaction centres (Roden *et al.* 1999), and partial photoinactivation of PS2 (Anderson *et al.* 1998, Niyogi 1999). However, this mechanism appears to protect leaves at certain threshold level of temperature and VPD. Beyond this level, as observed in June, the leaves may suffer from persistent photoinhibition, leading to severe inhibition of photosynthesis. The chronic photoinhibition in hot and dry season is reported in cerrado woody species (Franco and Lüttge 2002) though the temperatures in cerrados remained less than 40 °C. Franco and Lüttge (2002) have also implicated the role of photorespiration as a photoprotective mechanism in cerrado species on the basis of ratio of photorespiration to photosynthesis, which rose to 1.6 in one of the cerrado species, *Qualia gradiflora*. The other mechanisms for light driven sinks include Mehler-ascorbate peroxidase reaction (Lovelock and Winter 1996), though the actual contribution of each of these mechanisms has not been assessed in diurnal cycles yet.

In conclusion, *P. juliflora*, growing in northern India, is exposed to both low and high temperature stresses along with high irradiance during the year. To cope with this the plant produces two cohorts of leaves and each one faces either low or high temperature stress at the end of their life span. This ontogenic characteristic of *Prosopis* leaves along with protective processes such as radiation-less energy dissipation demonstrate that an efficient control of photochemical and non-photochemical quenching and adjustments in the partitioning of electron flow between assimilative and non-assimilative processes minimise the danger of photoinhibition.

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