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BRIEF COMMUNICATION

Effects of temperature and irradiance on photosystem activity during *Alhagi sparsifolia* leaf senescence

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Abstract

During the period of senescence of desert plant *Alhagi sparsifolia* Shap. the maximum photochemical quantum yield measured as variable to maximum fluorescence ratio (F_v/F_m) remained relatively high, although the number of active reaction centres per cross section (RCs) decreased significantly. The efficiency of electron acceptors beyond the primary quinone acceptor (Q_A) decreased. The effect of temperature and irradiance on photosystem activity was maximum after 6 d. Our results suggest that: *1*) the down-regulation of photosystem activity was due to the decline of both RCs and electron acceptance between plastoquinone (PQ) and cytochrome (cyt) *b6/f*; *2*) photosystem activity presented negative correlation with daily mean temperature, and *3*) reduction of daily sunshine period and increase of temperature at noon can stimulate the speed of senescence.

Additional key words: chlorophyll fluorescence, electron acceptors, environmental factors, photoperiod, reaction centres.

Leaf senescence is a typical physiological phenomenon in deciduous plants. It has been reported that photosynthetic capacity was inhibited by photochemical activities of photosystem (PS) I and II (Grover and Mohanty 1993), especially PSII activity (Gruszecki *et al*. 1991, Humbeck *et al*. 1996, Kumagai *et al*. 2009). Furthermore, in wheat the down-regulation of PSII occurred prior to that of net photosynthetic rate (Lu and Zhang 1998), and the loss of PSII function may be due to the decreased energy transfer from carotenoids to chlorophyll (Gruszecki *et al*. 1991), degradation of PSII reaction centre complex (Joshi *et al*. 1993), decreased efficiency of excitation energy capture by open PSII reaction centres (Königer *et al.* 2000), the closure of PSII reaction centres, the enhanced thermal dissipation in the PSII antennae (Lu *et al*. 2002) and blocked electron transport (Chen *et al*. 2010). Chlorophyll *a* (Chl *a*) fluorescence have been used to a non-destructive quantification of the damage to the leaf photosynthetic apparatus, particularly PSII, under abiotic stresses (Zhang *et al*. 2011). Furthermore, Keskitalo *et al*. (2005) showed that during senescence the most convenient way to assess decrease in photosynthesis activity was to measure chlorophyll fluorescence. However, few studies have provided a comprehensive analysis of fast Chl *a* fluorescence transients during leaf senescence under field, as presented here.

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Abbreviations: Chl - chlorophyll; cyt - cytochrome; DSD - daily sunshine duration; F_v/F_m - maximum photochemical efficiency; PI - performance index; PPFD - photosynthetic photon flux density; PQ - plastoquinone; PS - photosystem; Q_A - primary quinone acceptor; RCs - the number of active reaction centres per cross section; T_{max} - maximum temperature; T_{mean} - daily mean temperature; T_{min} - minimum temperature; ψEo - the quantum yield of electron transport.
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It was observed that irradiance was the main factor triggering leaf senescence (Keskitalo *et al*. 2005). However, very little is known about other factors modulating autumn senescence although low temperature and the length of the dark period may control senescence in aspen (Fracheboud *et al*. 2009). Because several factors, such as air temperature, day length and rainfall, often change at the same time under field experiments (Rosenthal and Camm 1997), the effects of individual environmental conditions on photosynthetic activity often cannot be distinguished.

In our experiments, the *Alhagi sparsifolia* Shap. grew at transition zone between Cele oasis and the southern fringe of Taklamakan sandy desert. One hundred of intact and mature leaves of similar size, and located at the same part of branches and position toward the sun were marked before measurement. The measurements were conducted every 5 d from 19 August (day of year 232) to 3 September and every 6 d from 3 to 27 September (day of year 271). Ten marked leaves were selected randomly for every measurement on sunny and breezy mornings. The measurement of Chl *a* fluorescence was conducted with adequately dark-adapted leaves for 20 min at room temperature (25 °C) using a plant efficiency analyzer (*Handy PEA*, *Hansatech*, King's Lynn, Norfolk, UK). Irradiance was 3 600 μmol m^{-2} s^{-1} to generate fast fluorescence curves expanding from O (taken as F_o) to P (F_m) for all the treatments. An analysis of the fast OJIP fluorescence rise has been developed, called as JIP-test (Strasser *et al*. 2010). A *WeatherHawk-500* (*Campbell Scientific,* Salt Lake City, USA) was set that automatically collected weather data every 15 min. The meteorological factors were evaluated by *SAS* software (*SAS*, Chicago, USA) by moving averages of three categories of temperature (T_{mean}, T_{max} and T_{min}), photosynthetically active radiation (PAR) and daily sunshine duration (DSD) measured on day 2, 4, 6, 8, 10, 12 and 14 preceding the fluorescence and pigments measurement. The calculation of DSD was according to World Meteorological Organization (2003) that the sunshine duration is the length of time in which the sunshine radiation falling on a plane perpendicular to the direction of the sun is greater or equal to 120 W m^{-2}. After the measurements of fluorescence, leaf area of ten leaves was scanned by *Delta-T Scan* (Cambridge, UK). The pigments were extracted with 80 % acetone, and determined using the a *UV-2550* spectrophotometer (*Shimadzu*, Kyoto, Japan).

With increasing senescence, the fluorescence intensities gradually decreased, with the extent of the decrease being bigger at P than that of at I level of OJIP curve and that at O level being the smallest (Fig. 1*A*). The variable to maximum fluorescence ratio (F_v/F_m, where $F_v = F_m - F_o$, or φP_o), an indicator of the quantum yield of primary photochemistry of PSII, decreased slightly with increasing senescence (Fig. 1*F,*), indicating the relative stability of primary charge separation in active reaction centres and maintaining electron transfer to Q_A although RCs decreased significantly (Fig. 1*G*). The slight decrease of F_v/F_m may be attributable to a mechanism that the excitation energy was partially absorbed by inactive reaction centers. It was documented that inactivation of water-splitting complex resulted in further reduction of PSII photochemical activity (Gruszecki *et al*. 1991, Joshi *et al*. 1993, Königer *et al*. 2000, Lu *et al*. 2002, Chen *et al*. 2010). The values of ΨE_o (Strasser *et al*. 2010) reflects the efficiency of electron acceptors of the chain which comprises the secondary quinone acceptor, plastoquinone (PQ), cytochrome (cyt) and plastocyanin (PC). The electron transport in PSI acceptor side was calculated as $\delta/(1 - \delta)$, where δ means probability with which an electron from the intersystem electron carriers is transferred to electron acceptors at the PSI acceptor side. The values of last two parameters significantly decreased (Fig. 1*F,G*) which showed that the efficiency of PSI electron acceptor side decreased. During the period of senescence, the decrease of fluorescence in I - P phase was progressively larger than that in J - I or O - J phases (Fig. 1*E*). The fluorescence in the J - I phase has been interpreted as reflecting the changes in the PQ pool (Schansker *et al*. 2003, Strasser *et al*. 2004) and the appearance of I - P phase is due to the kinetic bottleneck of the electron transport chain between PQ and cyt *b6/f* (Strasser *et al*. 2010). Furthermore, a theoretical study confirmed that the initial redox state of cyt *b559* strongly affect F_m (Lazár *et al*. 2005). The comparison of the extents of decrease for O - J, J - I and I - P phases indicated that the electron transfer chain corresponding to I - P rise was decreased in senescing leaf. These results demonstrated that leaf senescence could decrease the electron transfer between PQ and cyt *b6/f*, with subsequently inhibited Q_A^- reduction.

The photosynthetic performance index (PI) combines three independent functional steps of photosynthesis, the density of RCs in the Chl bed, excitation energy trapping and conversion to electron transport (Strasser *et al*. 2004). In this research the decline of PI (Fig. 1*H*) was mainly due to the decline of RCs and the efficiency of electron transport between PQ and cyt *b6/f*. With increasing senescence, the PI decreased significantly more than F_v/F_m. Thus PI can function as a convincing parameter to assess the heterogeneity of PSII in senescence of green plants. Our findings indicated that decrease of photochemical activity likely resulted from the decline in both RCs and electron accepting capacity of PQ and cyt *b6/f*.

From 4 August to 26 September, the daily temperature and PPFD generally decreased. During this period, there were no abnormal values and extreme weather condition like frosts or cold weather. The stepwise regression method was used to identify the important factors that determined actual relationship with dependent variable. Firstly, the tests of significance (*F*) of regression equations with increasing time step were significant at 0.01 level showing that there was a

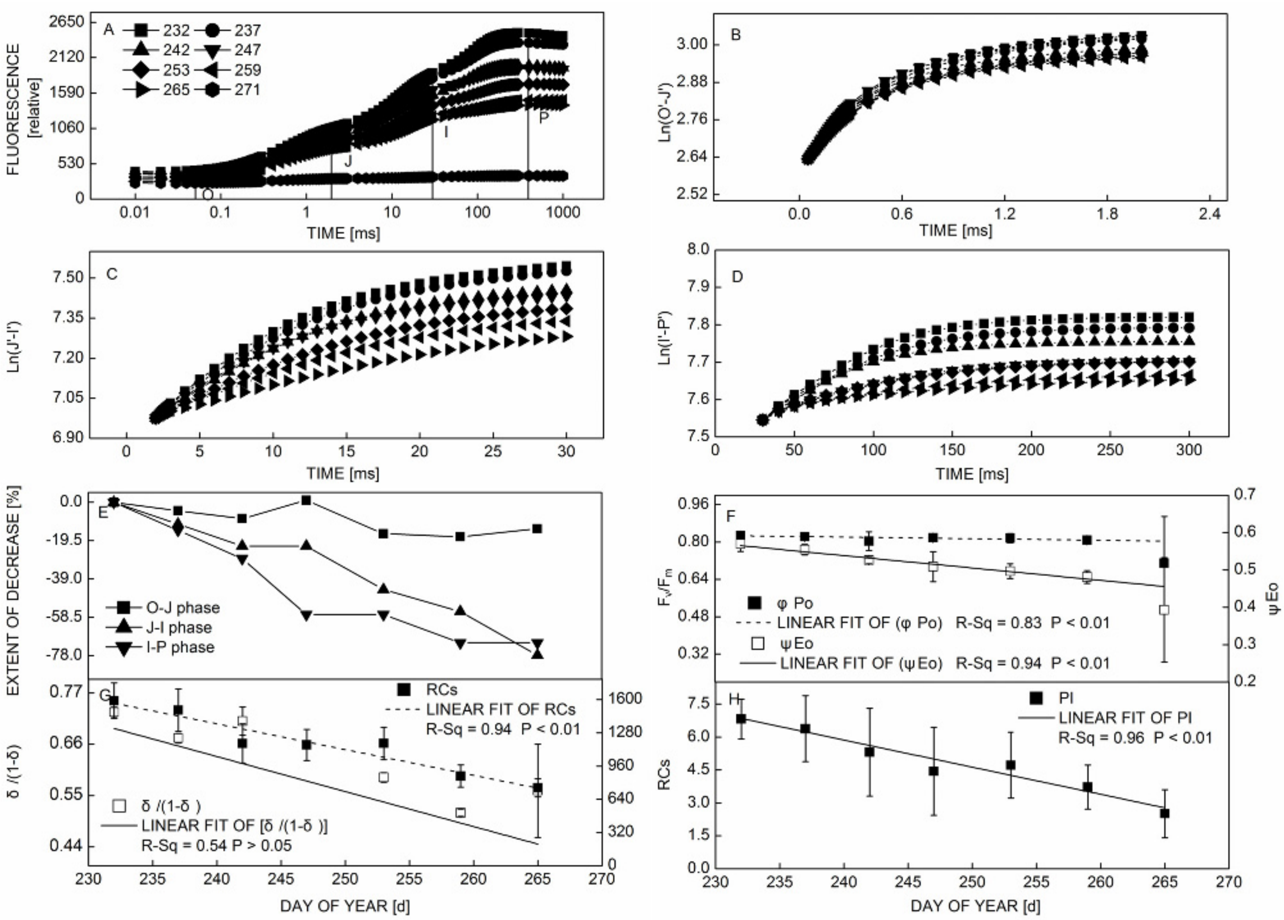

Fig. 1. Chl *a* fluorescence induction curves in senescing leaves for eight measuring days (n = 10) (*A*). The natural logarithm of O - J, J - I and I - P phases was presented on linear time scale from 0.03 ms to 2 ms, 2 ms to 30 ms and 30 ms to 300 ms, respectively, labeled as O´ - J´ (*B*), J´ - I´ (*C*) and I´ - P´ (*D*). The O´ - J´, J´ - I´ and I´ - P´ curves were drawn by shifting the O - J, J - I and I - P curves respectively, so that they start from the same value at O´, J´ and I´. In this way, the curves can be compared concerning their normalized values. The fitting equations for O´ - J´, J´ - I´ and I´ - P´ curves at each measurement day were modeled using linear equations with two un-knowns and the extent of the decrease of each O´ - J´, J´ - I´ and I´ - P´ curves was deduced based on the corresponding values on day of year 232 (*E*). The efficiencies/yields per absorption basis, which are defined as ratios of the energy fluxes, are shown (means ± SD, n = 10): F_v/F_m - the maximum quantum yield of primary photochemistry (*F*); ψEo - the efficiency of electron transport of intersystem chain (*F*); δ/(1 - δ) - the performance of PSI calculated for the electron transport segment between PQ and NADPH (*G*); RCs - the number of active PSII reaction centres per cross section (*G*); PI - photosynthetic performance index.

relationship between the selected variables and dependent variables. Adjusted correlation coefficients (Adj R-Sq) with increasing time step firstly increased then decreased, and peaked at approximately 10 d, indicating that the effect of daily mean temperature can explain 74.98 % of the variation in Chl content. The cumulated T_{mean} showing a positive correlation with Chl per area, further demonstrated that Chl degradation is temperature dependant, namely it can be enhanced more in cold weather than in warm weather. This finding was in accordance with conclusion drawn by Fracheboud *et al.* (2009).

Although Chl content corresponded to overall amounts of Chl-binding proteins, Chl content alone provide no direct evidence that the photosynthetic apparatus is functional (Keskitalo *et al*. 2005). Therefore, the direct indication of photosynthetic activity in autumn leaves is better for understanding the relationship between photosynthetic activity and meteorological factors. For PI, the *F*-tests at each time step showed significant relationship between PI and cumulated T_{mean} or DSD. The Adj R-Sq with increasing time step presented firstly increase then decrease, and tended to the peak at approximately day 6, indicating that the combined effect of independent variables can account for 96.17 % of the variation in PI. Secondly, at day 6 regressions between PI and three independent variables like T_{mean}, T_{max} and DSD were shown (P < 0.05). The influence of T_{mean} on photosynthetic activity during senescence was significantly larger than of other two factors.

In summary, this study demonstrated the characteristics of PSII and their relation with ambient temperature and irradiance during leaf senescence in desert plant, which may contribute to model autumn phenology. As reported by Fracheboud *et al*. (2009) and in accordance with our conclusion, the progression of autumn senescence is generally affected by average temperature and photoperiod, but senescence progression for different species may be dependent on their local environments, because the low temperature accelerated Chl degradation in European aspen and high temperature at noon impaired photochemical efficiency in desert plant *Alhagi sparsifolia*.

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