Ecol Res (2018) 33: 413–423
DOI 10.1007/s11284-018-1561-9

SPECIAL FEATURE

Climate Change and Biodiversity Conservation in East Asia as a token of memory for the 7th EAFES in Daegu, Korea

Sun Mi Je · Sun Hee Kim · Soo Young Woo

Responses of the photosynthetic apparatus of *Abies koreana* to drought under different light conditions

Received: 27 February 2017 / Accepted: 25 November 2017 / Published online: 23 January 2018

Abstract The threat of drought to trees is predicted to increase due to global warming. In a forest stand, the physiological responses of trees can differ depending on the light conditions. We analyzed photosynthetic rate, photopigment, and chlorophyll a fluorescence transient (OJIP test) of *Abies koreana* E.H. Wilson, under different light (full sunlight and 35 and 75% shading) and water conditions (well-watering, *W*; and no-watering, *NW*) to examine the combined effect of light and water. After 21 days of no-watering, we observed decreases in the photosynthetic rate and photopigment contents and quality, impairment of electron transfer from primary to secondary quinone acceptor, inactivation of reaction center, and lower photosynthetic performance index, especially under full sunlight. The time required for recovery after re-watering was also slower under full sunlight. In conclusion, the adverse effects of drought on light absorption and utility of *A. koreana* in the photosynthetic process were much greater under high light intensity compared to shading conditions, which alleviated these effects.

Keywords *Abies koreana* · Chlorophyll a fluorescence · Climate change · Drought · Shade

Introduction

Forests have experienced unequivocal climate warming in recent decades (IPCC 2013). Rising temperatures contribute to an increase in surface evapotranspiration; therefore, a change in the surface water balance is predicted (Knapp et al. 2015). Trees are considered vulnerable to drastic changes in soil moisture conditions because their roots cannot move freely. Although various forest disturbance factors (e.g., beetle attacks) could be involved in tree decline or mortality, drought related to global warming has been proposed as a major trigger (Allen et al. 2010; Smith et al. 2015). Furthermore, when a drought period is long, intense, or frequently occurring, it can lead to tree mortality (Brzostek et al. 2014; Cailleret et al. 2014).

In Korea, Korean fir (*Abies koreana*) in sub-alpine forests have suffered severe decline from the early 2000s. *Abies koreana* is categorized as an endangered species by the International Union for Conservation of Nature (IUCN) (Kim et al. 2011) and designated as a climate-sensitive biological indicator species (CBIS) in Korea (Lee et al. 2010). The most likely cause of *A. koreana* decline is related to the drought-induced by warming in early spring (Lim et al. 2007; Woo et al. 2008). However, knowledge regarding the physiological processes that lead to *A. koreana* mortality is limited. Therefore, intensive studies on physiological responses to environmental changes in *A. koreana* are required to understand and predict their responses to climate change, as well as for restoration.

The rapid decline of *A. koreana* has led to new environmental conditions in which the trees are exposed to more light. Therefore, it is necessary to examine the effect of light conditions on the physiological traits to determine the causes responsible for the increase in the decline rate of *A. koreana*. Light absorption and utilization are the first phases of photosynthesis, which are directly affected by changes in the light environment (Bjorkman 1981; Pearcy and Sims 1994). Consequently, the structural and functional properties of leaves are adapted to an efficient use light for tree survival and growth (Nobel 2009; Terashima et al. 2011; Vogelmann and Gorton 2014; Kwon and Woo 2016; Valladares et al. 2016). These traits respond sensitively to different light conditions depending on species-specific traits such as extent of shade tolerance and sun/shade dependence

S. M. Je · S. H. Kim (✉)
Department of Forest Conservation, National Institute of Forest Science, Seoul 02455, Republic of Korea
E-mail: sands02@korea.kr
Tel: +82-2-961-2617

S. Y. Woo
Division of Environmental Horticulture, Department of Natural Science, University of Korea, Seoul 02504, Republic of Korea

(Murchie and Horton 1997; Valladares et al. 2000; Fini et al. 2014; Sancho-Knapik et al. 2014).

Changes in leaf traits to adapt to varying light conditions could affect drought sensitivity. For example, Jiménez et al. (2009) reported that *Quercus suber* trees grown in moderate shade (15% light) have a higher tolerance to drought conditions than those grown in deep shade (1% light). *Fraxinus ornus* trees display higher dissipation of excess radiant energy (non-photochemical quenching) under high light irradiance and overcome oxidative damage to a greater extent compared to the trees grown in shade under drought (Fini et al. 2014).

Chlorophyll a fluorescence transient measurement (OJIP test) has been reported to be a sensitive and reliable method to detect the changes in the photosynthetic apparatus (Schansker et al. 2005; Shao et al. 2010; Wang et al. 2012). The OJIP fluorescence transient reflects the state of Q_A, Q_B, and PQ pool. Therefore, it is possible to provide detailed information on the functional traits of the photosynthetic apparatus such as absorption and trapping photons, dissipation of excess energy, electron transport, and level of photosynthetic performance (Strasser et al. 2004; Lepeduš et al. 2011; Stirbet 2011). Drought conditions are known to reduce the ability of absorption and trapping photons, electron transport by inactivated and/or damaged reaction centers and increases the quenching reaction center to dissipate of excess energy (van Rensburg et al. 1996; Gallé et al. 2007; Albert et al. 2011; Wang et al. 2012). However, the interactive effect of light and drought on the photosynthetic apparatus has not been well-addressed. In particular, drought responses of *A. koreana* growing under different light conditions have not been previously reported.

We examined the changes in functional traits of the photosynthetic apparatus using chlorophyll fluorescence traits to better understand the response of *A. koreana* to light and drought conditions. We also analyzed the changes in photosynthetic rate, and composition and amount of photopigments under different light regimes and water status in *A. koreana* seedlings, which are more sensitive to environmental stresses than adult plants. We hypothesized that the photosynthetic apparatus of *A. koreana* would change under different light conditions and affect the response to progressive drought and recovery.

Materials and methods

Plant material and experimental conditions

This experiment was conducted at the National Institute of Forest Science (NIFoS), Seoul, Korea (37°35′N, 127°2′W) from April 4 to August 26, 2014. Three-year-old seedlings of *A. koreana* were planted in 2.5-L pots (one seedling per pot) containing forest soil. After 2 weeks, the seedlings were exposed to artificial shade levels produced through the use of different shading nets, fixed in wireframe facilities with a transparent roof as a rain shelter to exclude the effects of rain. These nets allowed for the 35% shading (1,000–1,400 µmol m^{-2} s^{-1}, min–max) and 75% shading (200–400 µmol m^{-2} s^{-1}) of full sunlight (1,500–1,900 µmol m^{-2} s^{-1}). The photosynthetic photon flux density (PPFD) was converted from light intensity using the HOBO pendant temperature/light data logger (UA-002-64, Onset, MA, the USA) according to Wagner and McGraw (2013). Temperature and relative humidity readings were recorded for the shading treatments every 10 min using a HOBO Pro v2 logger (U23-002, Onset, MA, the USA). Mean air temperature and relative humidity for full sunlight, 35% shading, and 75% shading were 30.2 ± 2.1 °C and 61.4 ± 9.0%, 29.5 ± 2.8 °C and 60.5 ± 10.2%, and 30.4 ± 2.6 °C and 62.0 ± 11.1%, respectively. Light intensity, mean air temperature, and relative humidity were measured at the upper extremity of plants between 08:00 and 18:00 h on 24 clear days during the experimental period.

Watering treatments

The seedlings were watered daily to field capacity until the beginning of the drought experiment. On the first day of the experiment (July 10, 2014), half of the seedlings from each shading treatment were selected for well-watering treatment (*W*), and the other half were no-watering treatment (*NW*) subjected to a progressive drought. When one of the light treatments reached a mean photosynthetic rate (net CO_2 gas exchange rate on leaf dry weight basis) of 0 µmol g^{-1} s^{-1} or less due to the drought, all the *NW* treatments were re-watered. During the experiment, soil volumetric water content (SVWC, %) was measured daily twice (Field Scout TDR 100, Spectrum Technologies, Inc., Plainfield, IL, the USA). The SVWC in *W* was maintained between 12 and 20% during the experiment. However, the SVWC in the *NW* treatment drastically decreased until 15 days after no-watering and was maintained below 3% for 1 week until re-watering occurred (Fig. 1).

Photosynthetic rate measurements

Measurements of photosynthetic rate (P_N) were conducted weekly from the start of the watering treatment. Recently expanded terminal leaves were chosen and repetitively measured using a portable photosynthesis systems equipped with light-emitting diode (LED) light sources and the standard 2 × 3 cm chambers (Li-6400XT and Li-6400-02B LED, Li-Cor Inc., Lincoln, the USA) during the experimental period. During measurements, CO_2 concentration, temperature in the chamber, flow rate of air, and PPFD were maintained at 400 µmol mol^{-1}, 27 °C, 500 µmol s^{-1}, and 1,000 µmol m^{-2} s^{-1}, respectively. After the experiment, measured needles were removed from the trees and dried and

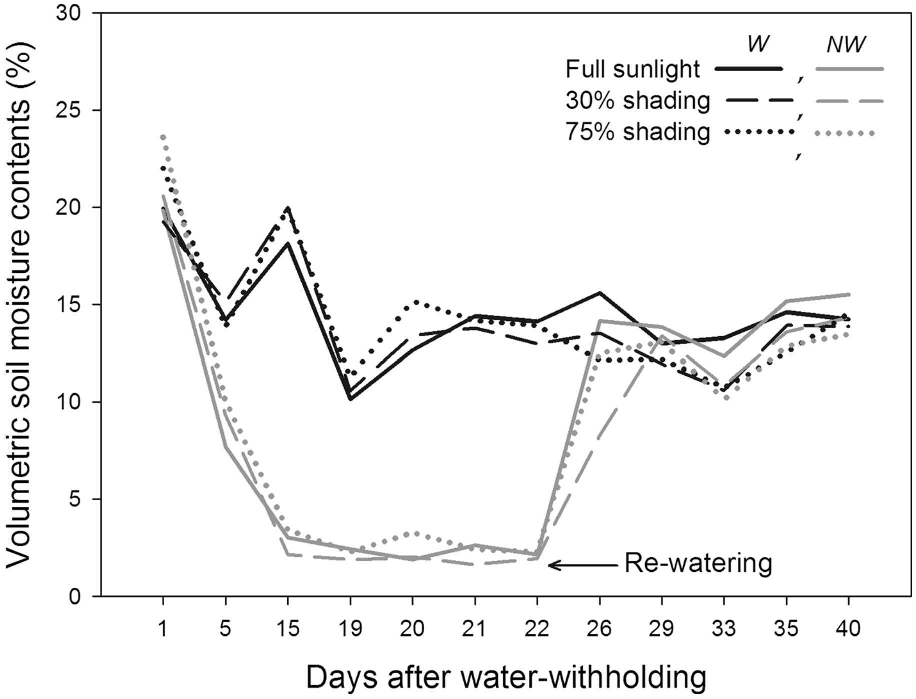


Fig. 1 The average volumetric soil moisture contents in each treatment. Black dash and grey dash lines indicate well-watering (*W*) and no-watering (*NW*), respectively

weighed for calculation of the P_N using needle dry weight according to von Caemmerer and Farquhar (1981).

Photopigment analysis

Photopigments were measured after no-watering for 21 days. The fresh needle disk (0.1 g) was immersed in 10 ml of dimethyl sulfoxide (DMSO) (99%) for 6.5 h at 65 °C. The absorbance of its extracts was measured using a spectrophotometer (DU730 UV VIS Beckman Coulter, the USA) at wavelengths of 470, 645, and 663 nm for chlorophyll a (Chl_a), chlorophyll b (Chl_b), carotenoid (Car.), and xanthophyll (Xan.) contents, respectively. Chlorophyll and accessory pigment contents were calculated according to Wellburn and Lichtenthaler (1984).

Chlorophyll a fluorescence transient analysis

Measurements of chlorophyll a fluorescence transient (OJIP test) were performed at the same time of photosynthetic rate measurements. Chlorophyll a fluorescence transient was measured using a Pocket-PEA fluorimeter (Hansatech Instruments Ltd., the UK) on plants that were dark adapted for at least 30 min. A total of 5–8 seedlings per treatment were used. The Pocket-PEA fluorimeter was at O (50 µs), J (2 ms), and I (30 ms) as the intermediate stage, and P (300 ms) as the peak. The obtained data were used in the OJIP test (Strasser et al. 2004) to calculate the following parameters of photosystem II (PSII) photochemistry (Table 1). Data are presented as spider plots, indicating the mean of the relative change of the selected parameters in relation to their corresponding well-watering values. ΔF_{IP} (fluorescence amplitude of the I to P phases) was calculated using the difference in P and I fluorimetry (Ceppi et al. 2012).

Statistical analysis

All data were subjected to one-way analysis of variance (ANOVA) using SPSS 13.0 (SPSS Inc., Chicago, IL, the USA) to determine the difference between treatments. Duncan's multiple range tests were used to detect significant differences between means at a significance level of $P < 0.05$.

Results

Photosynthetic rate

Although P_N of all light treatments showed a decreasing tendency due to drought, P_N of 75% shading showed no difference between *W* and *NW* until the 19th day of no-watering. The first time that the photosynthetic rate

Table 1 Definitions and explanations of selected OJIP test parameters

Fluorescence parameters	
F_0	Fluorescence intensity at 50 μs (O step)
F_M	Maximal fluorescence intensity (P step)
F_J	Fluorescence intensity at 2 ms (J step)
F_I	Fluorescence intensity at 30 ms (I step)
F_V/F_0	Ratio of photochemical and non-photochemical de-excitation fluxes of excited chlorophyll $F_V = (F_M - F_0)/F_0$
ΔF_{IP}	Fluorescence amplitude of the I to P rise $\Delta F_{IP} = F_P - F_I$
V_I	Relative variable fluorescence at the I-step $V_I = (F_I - F_0)/(F_M - F_0)$
V_J	Relative variable fluorescence at the J-step $V_J = (F_J - F_0)/(F_M - F_0)$
N	Turnover number of primary quinone acceptor (Q_A) $N = S_m \times (dV/dt_0)/V_J$
dV/dt_0	Slope of the induction curve from F_0 to F_M $dV/dt_0 = 4(F_{300\ \mu s} - F_0)/(F_M - F_0)$
Quantum efficiency/flux ratios	
ΦP_0	Maximum yield of primary photochemistry, equal to F_V/F_M $\Phi P_0 = (F_M - F_0)/F_M$
Ψ_0	Probability of a trapped exciton moving an electron beyond Q_A^- $\Psi_0 = (1 - V_J)$
ΦE_0	Probability of an absorbed exciton moving an electron beyond Q_A^- $\Phi E_0 = [(F_M - F_0)/F_M]/(1 - V_J)$
Density of reaction centers	
RC/CS	Relative number of active PSII reaction centers per excited cross-section $RC/CS = \Phi P_0[V_J/(dV/dt_0)]F_0$
Specific fluxes per active PSII reaction center	
ABS/RC	Absorption flux, effective antenna size of an active reaction center $ABS/RC = (dV/dt_0) \times (1/V_J) \times [1/\Phi P_0]$
DI_0/RC	Dissipation flux $DI_0/RC = (ABS/RC) - (TR_0/RC)$
TR_0/RC	Trapped energy flux leading to a reduction of Q_A $TR_0/RC = (dV/dt_0) \times (1/V_J)$
ET_0/RC	Electron transport flux further than Q_A $ET_0/RC = (dV/dt_0) \times (1/V_J) \times \Psi_0$
Area above the induction curve	
S_m	Normalized area $S_m = AREA/(F_M - F_0)$
Performance index	
PI_{abs}	Performance index based on absorption. Efficiency of energy conservation from absorbed photons to reduction of intersystem electron carriers $PI_{abs} = (RC/ABS) \times [(\Phi P_0) \times (1 - \Phi P_0)] \times [\Psi_0/(1 - \Psi_0)]$

reached 0 μmol g^{-1} s^{-1} was on the 21st day of no-watering under full sunlight. Moreover, no recovery of P_N was observed under full sunlight until the 7th day after re-watering, whereas P_N was recovered on the 4th day after re-watering for other light treatments (35 and 75% shading) (Fig. 2).

Photopigment characteristics

Chl_T and Car. + Xan. were significantly increased with an increase in shading under *W*. The same patterns were also observed with *NW*. Decrease tendency in Chl_a/Chl_t and increase tendency in Chl_b/Chl_t also showed an increase in shading under *W*. However, these tendencies were not observed under light treatment combined with *NW*. A significant difference between *W* and *NW* for Chl_a/Chl_b was observed only under full sunlight (Table 2).

Chlorophyll a fluorescence transient traits (OJIP test)

The OJIP curves reflect the major changes in photosynthetic electron transport. *NW* showed lower fluorescence values in the OJIP curves than *W* especially in phases I and P. This indicates that drought led to inhibition of electron transport from primary (Q_A) to secondary quinone acceptor (Q_B). These differences in the IP phase (ΔF_{IP}) between *W* and *NW* in 75% shading were the smallest among light treatments (full sunlight and 35% shading) (Fig. 3).

The patterns of spider-plot presentation in chlorophyll a fluorescence transient parameters showed similar shapes under full sunlight and 35% shading by water treatment. However, those values were different under 75% shading (Fig. 4). Similarly, under full sunlight and 35% shading, the reductions in yield (ΦP_0, Ψ_0, and ΦE_0), area (S_m and N), performance index (PI_{abs}), and electron transport flux further than Q_A (ET_0/RC) and the increases in F dynamic (F_0, V_J, and dV/dt_0) and

Fig. 2 Changes in the photosynthetic rate (P_N) in the needles of *Abies koreana* seedlings grown in different light (full sunlight: **a**; 35% shading: **b**; 75% shading: **c**) and water treatments (*W*: well-watering; *NW*: no-watering). Values are mean and error bars represent standard deviation from the mean ($n = 7$). The single asterisk indicates significant difference at $P < 0.05$ by ANOVA (DUNCAN)

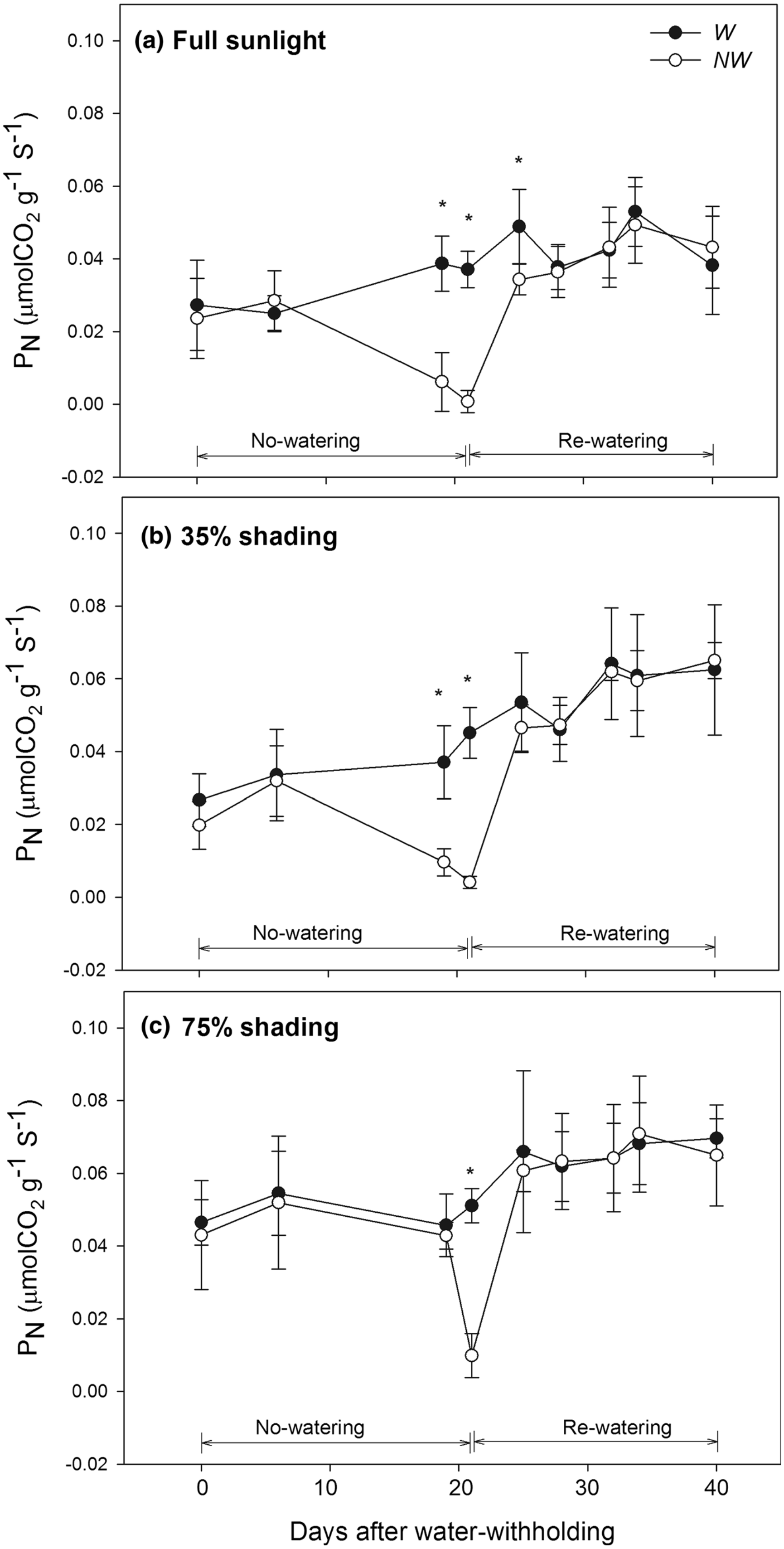


Table 2 Photopigment content and quality in the needles of *Abies koreana* seedlings grown in different light and water treatments (*W*: well-watering; *NW*: no-watering) at the end of drought (21st day of no-watering)

	Chl_T	Chl_a/Chl_T	Chl_b/Chl_T	Chl_a/Chl_b	Car. + Xan.
W					
Full sunlight	1.001 ± 0.151^c	0.785 ± 0.006^a	0.215 ± 0.006^c	3.645 ± 0.142^a	0.243 ± 0.032^c
35% shading	1.539 ± 0.074^b	0.776 ± 0.002^b	0.224 ± 0.002^b	3.459 ± 0.045^b	0.357 ± 0.018^{ab}
75% shading	1.859 ± 0.081^a	0.764 ± 0.002^c	0.236 ± 0.002^a	3.244 ± 0.043^c	0.394 ± 0.016^a
NW					
Full sunlight	0.745 ± 0.015^d	0.767 ± 0.001^c	0.233 ± 0.001^a	3.284 ± 0.020^c	0.201 ± 0.008^c
35% shading	1.493 ± 0.237^b	0.778 ± 0.003^b	0.222 ± 0.003^b	3.500 ± 0.062^b	0.325 ± 0.055^b
75% shading	1.821 ± 0.078^a	0.763 ± 0.003^c	0.237 ± 0.003^a	3.218 ± 0.055^c	0.398 ± 0.017^a

Values are mean and error bars represent standard deviation from the mean ($n = 4$). Different letters indicate significant difference at $P < 0.05$ by ANOVA (DUNCAN)

Chl_T: total chlorophyll (mg g^{-1}); Chl_a/Chl_T: ratio of chlorophyll a to total chlorophyll; Chl_b/Chl_T: ratio of chlorophyll b to total chlorophyll; Chl_a/Chl_b: ratio of chlorophyll a to b; Car. + Xan.: accessory pigments as sum of carotenoid and xanthophyll (mg g^{-1})

parts of flux per reaction center (RC) (ABS/RC, DI_0/RC, TR_0/RC) were significant in *NW* on the 21st day of no-watering (Fig. 4a). Under 75% shading, only the reduction in PI_{abs} caused by *NW* was similar to the other light treatments (full sunlight and 35% shading) (Fig. 4a). On the 11th day after re-watering, decreases in ΦE_0 and PI_{abs} and increases in V_J and parts of flux per RC (ABS/RC, DI_0/RC, TR_0/RC) were observed under full sunlight and *NW* (Fig. 4b). At the same time, an increase in DI_0/RC was observed only under 35% shading, and there were no significant differences between *W* and *NW* in the case of 75% shading (Fig. 4b). On the 13th day after re-watering, there were no significant differences in any of the light treatments (Fig. 4c). Apparent recovery by re-watering was observed on the 19th day after re-watering, as indicated by the same spider-plot pattern between *W* and *NW* (Fig. 4d).

Discussion

Effects of different light conditions on the photosynthetic rate under drought and re-watering

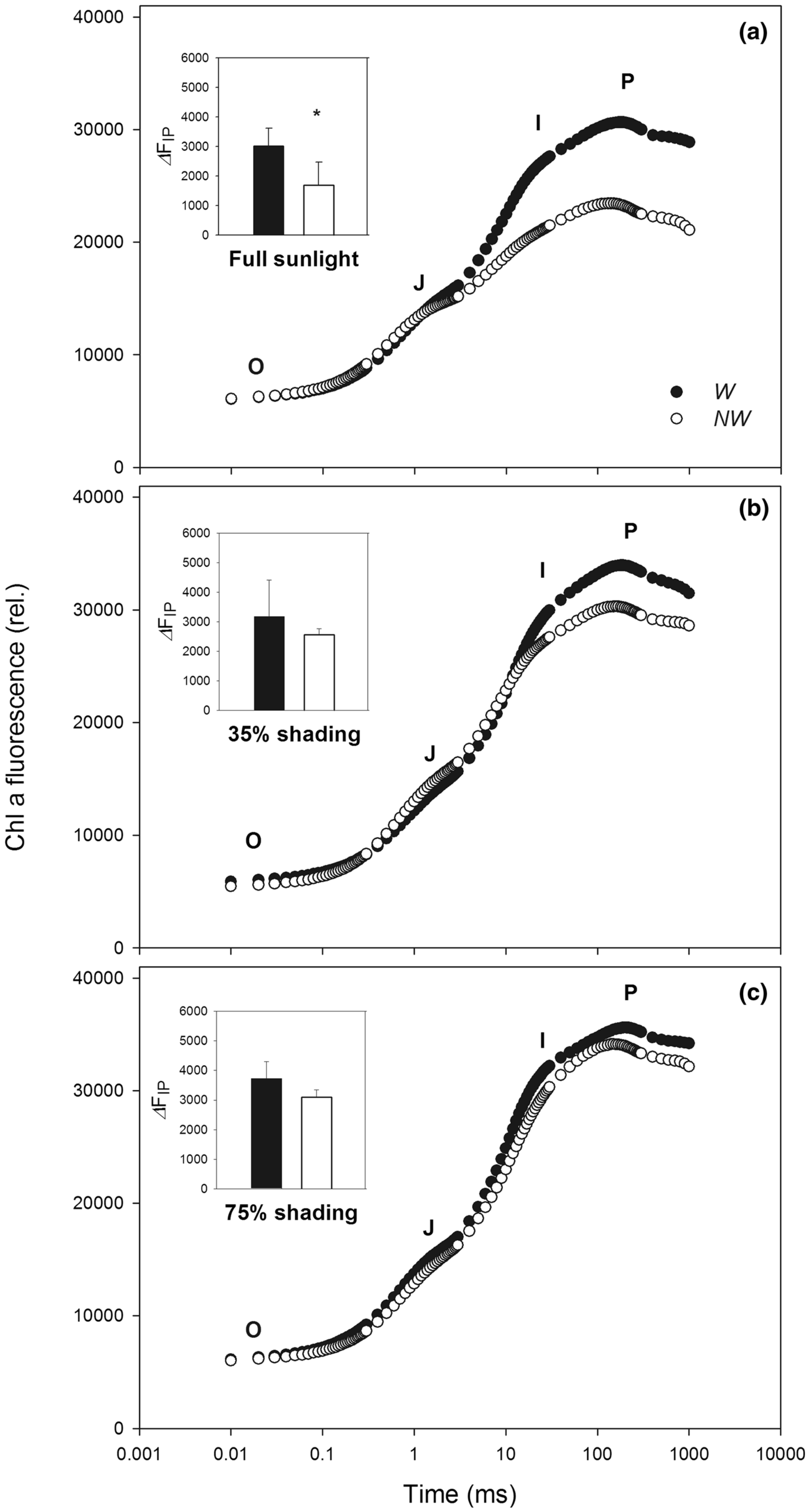
P_N decreased with an increase in the water-withholding treatment period. However, the pattern change was different depending on the light treatment. P_N in 75% shading appeared to have no significant differences between *W* and *NW* until the 19th day of water withholding whereas those under full sunlight and 35% shading showed significant decline at that time (Fig. 2). Drought usually induces stomatal closure to preserve the water in the plant which contributes to the initial decrease in P_N by restricting CO_2 input into the leaf (Rodriguez-Dominguez et al. 2016). The decrease in P_N could induce a decreased demand for adenosine triphosphate (ATP) and nicotinamide adenine dinucleotide phosphate (NADPH) in the Calvin-Benson cycle and led to a redox back pressure on PSII (Medrano et al. 2002). Under continuing light-driven electron transport, imbalances between electron use and energy consumption cause the generation of reactive oxygen species (ROS) directly and/or indirectly (Asada 2006). If ROS cannot be scavenged sufficiently, the photosynthetic apparatus can be damaged due to oxidative stress (e.g., destruction of cell structure and components) (Asada 1999; Flexas and Medrano 2002). Therefore, as the extent and period of water stress increase, P_N reduces due to the impaired photosynthetic apparatus (Flexas et al. 2006; Xu et al. 2010).

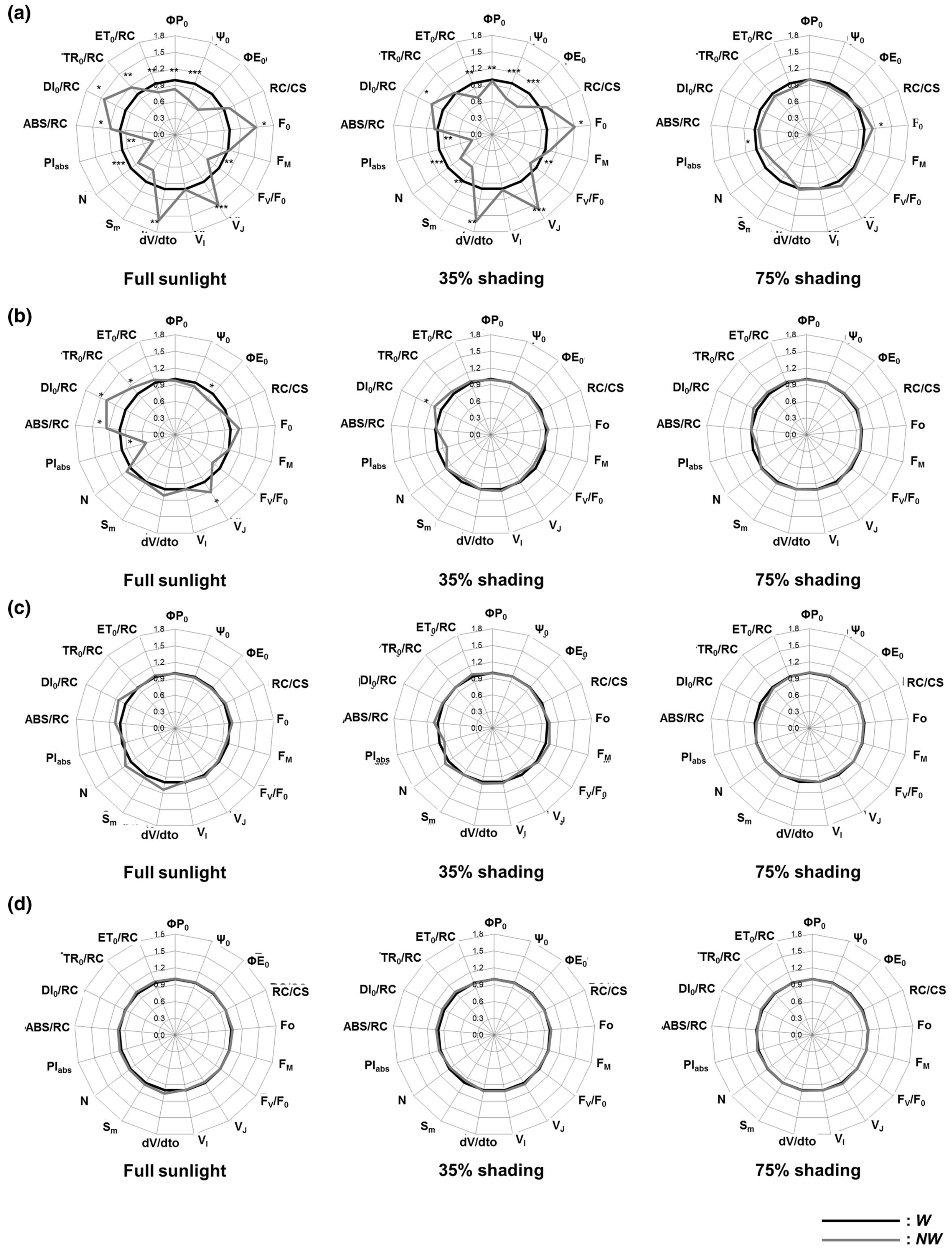
In the present study, reductions in the amount and quality of photopigment and the low capability of light capture and utilization implied that damages were preceded by drought especially under full sunlight (Table 2 and Figs. 3, 4). In *A. koreana*, full sunlight and 35% shading could likely be the conditions that imposed excessive light energy input. Thus, photoinhibition may have caused a decrease in P_N (Powles 1984; Alves and Magalhães 2002). The excess photon energy received by chlorophyll molecules are utilized during photosynthesis or dissipated by non-photochemical quenching (NPQ). However, if the absorption of light exceeds the utilization during photochemical conversion, it is exacerbated the photoinactivation of PSII, which is damaged or incorrectly assembled chlorophyll protein complexes (Santabarbara et al. 2002; Oguchi et al. 2011). Unlike 35% shading and full sunlight treatment, the 75% shading treatment delayed the time when P_N reduced to 0 µmol g^{-1} s^{-1} due to drought and showed rapid recovery after re-watering (Fig. 2). These results indicate that the effect of drought on photosynthesis in *A. koreana* depends on light conditions.

Changes in photopigment under different light and water conditions

Both Chl_T and accessory pigments (Car. + Xan.) in *A. koreana* significantly increased under shade treatments (Table 2) which indicated an adaptive response to low light conditions. A higher level of Chl_T and Car. + Xan. per leaf mass unit in shade treatments were similar to those previously described in *Abies alba* (Lichtenthaler et al. 2007), another coniferous tree (Wyka et al. 2008; Barsi et al. 2009), and other broadleaf species

Fig. 3 Effects on the kinetics of the OJIP transients and fluorescence amplitude of the I to P phase (ΔF_{IP}) measured in the needles of *Abies koreana* seedlings grown in different light (full sunlight: **a**; 35% shading: **b**; 75% shading: **c**) and water treatments (*W*: well-watering; *NW*: no-watering) at the end of drought (21st day of no-watering). Black circles and bars indicate *W*, and white circles and bars indicate *NW*. Values are mean ($n = 5$–7) and the single asterisk indicates a significant difference at $P < 0.05$ by ANOVA (DUNCAN)




(a)
(b)
(c)
(d)
ΦP0
Ψ0
ΦE0
RC/CS
F0
FM
FV/F0
VJ
VI
dV/dto
Sm
N
PIabs
ABS/RC
DI0/RC
TR0/RC
ET0/RC
0.0
0.3
0.6
0.9
1.2
1.5
1.8
*
**
***
Full sunlight
35% shading
75% shading
: W
: NW

◀ **Fig. 4** Spider-plot of OJIP parameters in the needles of *Abies koreana* seedlings grown in different light (full sunlight; 35% shading; 75% shading) and water treatments (*W*: well-watering; *NW*: no-watering) on the 21st (**a**) day of no-watering and the 11th (**b**), 13th (**c**), and 19th (**d**) days after re-watering. Values are mean ($n = 5$–7) and the single asterisk indicates a significant difference at $P < 0.05$ by ANOVA (DUNCAN)

(Lichtenthaler et al. 2007; Sarijeva et al. 2007). Accessory pigments are known to be potent quenchers of ROS (Asada 1999). When ROS in trees increase under unhealthy environmental conditions including drought, it plays an essential role in protecting the photosynthetic apparatus (Foyer and Shigeoka 2011; Jahns and Holzwarth 2012). Thus, under severe drought conditions, relatively lower accessory pigment contents under full sunlight compared to shade conditions (35 and 75% shading) would not be sufficient to scavenge the ROS increase. These conditions could have resulted in the low content of photopigment under combined treatment of full sunlight and *NW*.

A decrease in Chl_a/Chl_b with increasing chlorophyll b (Chl_b/Chl_T) was also observed in *W* subjected to shade treatments which implied an enhancement of the efficiency of blue light absorption under reduced light conditions (Yamazaki et al. 2005). Shade tolerant species have a higher photosynthetic capacity and can maintain their growth rates under shading conditions compared to intolerant species (Schrader et al. 2006; Valladares and Niinemets 2006). The observed responses can be assigned to the adaptive ability of *A. koreana* to cope with shade as shade tolerant species, and these responses led to a reduction in the non-stomatal limitation in terms of the efficiency of light capture and therefore, affected the photosynthetic rate in *NW*.

Changes in chlorophyll a fluorescence transient parameters under different light and water conditions

All treatments exhibited the typical polyphasic OJIP increases. However, OJIP curves indicated a reduction in shape due to drought especially in the IP phase (Fig. 3). The IP phase depends not only on the transient block on the acceptor side of photosystem I (PSI) but also on the flow of the electrons originating in PSII through PSI (Schansker et al. 2005). Therefore, IP phase amplitude can be used as an indicator of PSI content and activity (Ceppi et al. 2012). We calculated fluorescence amplitude of the I to P rise (ΔF_{IP}) to analyze elaborate differences in the IP phase. Interestingly, ΔF_{IP} was not affected by drought under 35 and 75% shading. ΔF_{IP} of full sunlight was low with both water treatments. Therefore, it can be concluded that PSI was less damaged even under drought due to the combination of shade conditions.

The changes in fluorescence parameters from the OJIP curves varied greatly between *W* and *NW* with the increase in light intensity under *NW* (Fig. 4). In the case of specific fluxes per active PSII reaction center referring to its function, the parameters describing absorption (ABS/RC), trapping (TR_0/RC), and dissipation of excess energy (Di_0/RC) were higher. Moreover, the electron transport beyond Q_A^- (ET_0/RC) was lower in *NW* than those of *W* under full sunlight and 35% shading on the last day of no-watering (Fig. 4). The increase in functional antenna size (high ABS/RC) indicated the presence of a non-Q_A reducing reaction center. Strasser et al. (2004) suggested a possibility that non-Q_A reducing reaction centers act as heat sinks. Similarly, we also showed the increase in Di_0/RC by drought under full sunlight and 35% shading in our study. Furthermore, the capability for electron transport beyond Q_A^- was impaired (low ET_0/RC) which indicated that electron transfer was reduced from Q_A^- to Q_B. The slope of the induction curve from F_0 to F_M (dV/dt_0) also increased, and implied inhibition of reoxidation of Q_A^- to Q_B by drought. These results were related to the accumulation of reduced primary plastoquinone (Q_A^-) and inactivation of RC which were confirmed by the increases in V_j, N, and S_m by drought under full sunlight and 35% shading.

The presence of non-Q_A reducing centers and a low electron transportation rate from Q_A to Q_B which are considered to be downregulation mechanisms dissipated the excess absorbed light in a controlled way. These mechanisms could protect the photosynthetic apparatus from photo-oxidation (Li et al. 2015). Matsubara and Chow (2004) and Vass and Cser (2009) also suggested that inactivation of RC is related to quenching reaction in terms of photoprotection, and prevents the photosynthetic apparatus from irreparable damage. This strategy could allow resilience to drought stress after re-watering. In consistent with our results, the photosynthetic apparatus was less damaged by drought, and it was rapidly restored by re-watering in drought-tolerant species (Gallé et al. 2007; Flexas et al. 2009).

The maximum quantum yield of primary photochemistry (ΦP_0) and photosynthetic performance index (PI_{abs}) are often used to gauge the occurrence and extent of changes in physiological responses in plants (Bussotti et al. 2007; Lepeduš et al. 2011; Wang et al. 2012). Many studies have reported a positive correlation between ΦP_0 or PI_{abs} and drought stress (Shao et al. 2010; Rathod et al. 2011). However, ΦP_0 occasionally only responds to severe stress conditions (Oukarroum et al. 2007; Wang et al. 2012) whereas PI_{abs} is more sensitive to stress (Bussotti et al. 2007; Wang et al. 2012). In our study, PI_{abs} was one of the indicators of drought effect on *A. koreana* under all light conditions. All fluorescence parameters indicated that the photosynthetic apparatus of *A. koreana* recovered from drought from the 13th day after re-watering. This recovery was also observed in the photosynthetic rate (Figs. 2, 4c). Thus, we can conclude that full sunlight conditions aggravate the damage to the photosynthetic apparatus during drought periods, although a complete recovery from water stress can be achieved after re-watering regardless of light conditions.

Conclusions

The photosynthetic apparatus of three-year-old seedlings of *A. koreana* grown under different light conditions indicated different responses to drought. Under full sunlight, a more impaired photosynthetic apparatus was observed during drought periods. Although the ability for light absorption and utilization and P_N in all light treatments was recovered after re-watering, *A. koreana* under full sunlight exhibited the lowest photopigment content and quality, PSII activities, and P_N compared to those under other light conditions during drought. Taken together, these results indicate that seedlings of *A. koreana* grown under high light intensity could be more vulnerable to drought events, and shading could decrease the sensitivity to drought by alleviating water stress.

Acknowledgements This study was supported by research grants from the National Institute of Forest Science (Project FE0100-2017-03).

References

Albert KR, Mikkelsen TN, Michelsen A, Ro-Poulsen H, van der Linden L (2011) Interactive effects of drought, elevated CO_2 and warming on photosynthetic capacity and photosystem performance in temperate heath plants. J Plant Physiol 168(13):1550–1561

Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M, Kitzberger T, Rigling A, Breshears DD, Hogg ET (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For Ecol Manag 259:660–684

Alves PLCA, Magalhães CAN (2002) The phenomenon of photoinhibition of photosynthesis and its importance in reforestation. Bot Rev 68(2):193–208

Asada K (1999) The water-water cycle in chloroplasts: scavenging of active oxygens and dissipation of excess photons. Annu Rev Plant Biol 50:601–639

Asada K (2006) Production and scavenging of reactive oxygen species in chloroplasts and their functions. Plant Physiol 141:391–396

Barsi DC, Major JE, Mosseler A, Campbell M (2009) Genetic variation and control of chloroplast pigment concentrations and related needle-level traits in *Picea rubens*, *Picea mariana*, and their hybrids: moisture and light environmental effects. Trees 23:555–571

Bjorkman O (1981) Response to different quantum flux densities. In: Lange OL, Nobel PS, Osmond CB, Ziegler H (eds) Physiological plant ecology I. Response to the physical environment, encyclopedia of plant physiology, new series, 12A. Springer, Berlin, pp 57–107

Brzostek ER, Dragoni D, Schmid HP, Rahman AF, Sims D, Wayson CA, Johnson DJ, Phillips RP (2014) Chronic water stress reduces tree growth and the carbon sink of deciduous hardwood forests. Glob Change Biol 20:2531–2539

Bussotti F, Strasser RJ, Schaub M (2007) Photosynthetic behavior of woody species under high ozone exposure probed with the JIP-test: a review. Environ Pollut 147:430–437

Cailleret M, Nourtier M, Amm A, Durand-Gillmann M, Davi H (2014) Drought-induced decline and mortality of silver fir differ among three sites in Southern France. Ann For Sci 71:643–657

Ceppi MG, Oukarroum A, Çiçek N, Strasser RJ, Schansker G (2012) The IP amplitude of the fluorescence rise OJIP is sensitive to changes in the photosystem I content of leaves: a study on plants exposed to magnesium and sulfate deficiencies, drought stress and salt stress. Physiol Plant 144:277–288

Fini A, Ferrini F, Ferdinando MD, Brunetti C, Giordano C, Gerini F, Tattini M (2014) Acclimation to partial shading or full sunlight determines the performance of container-grown *Fraxinus ornus* to subsequent drought stress. Urban For Urban Green 13(1):63–70

Flexas J, Medrano H (2002) Drought-inhibition of photosynthesis in C3 plants: stomatal and non-stomatal limitations revisited. Ann Bot 89:183–189

Flexas J, Ribas-Carbó M, Bota J, Galmés J, Henkle M, Martínez-Cañellas S, Medrano H (2006) Decreased Rubisco activity during water stress is not induced by decreased relative water content but related to conditions of low stomatal conductance and chloroplast CO_2 concentration. New Phytol 172:73–82

Flexas J, Barón M, Bota J, Ducruet J-M, Gallé A, Galmés J, Jiménez M, Pou A, Ribas-Carbó M, Sajnani C, Tomás M, Medrano H (2009) Photosynthesis limitation during water stress acclimation and recovery in the drought-adapted *Vitis* hybrid Richter-110 (*V berlandieri* × *V rupestris*). J Exp Bot 66(8):2361–2377

Foyer CH, Shigeoka S (2011) Understanding oxidative stress and antioxidant functions to enhance photosynthesis. Plant Physiol 155:93–100. https://doi.org/10.1104/pp.110.166181

Gallé A, Haldimann P, Feller U (2007) Photosynthetic performance and water relations in young pubescent oak (*Quercus pubescens*) trees during drought stress and recovery. New Phytol 174:799–810

IPCC (2013) The Fifth Assessment Report (AR5) climatic change: the physical science basis. Intergovernmental Panel on Climate Change

Jahns P, Holzwarth AR (2012) The role of the xanthophyll cycle and of lutein in photoprotection of photosystem II. Biochim Biophys Acta Bioenerg 1817:182–193

Jiménez MD, Pardos M, Puértolas J, Kleczkowski LA, Pardos JA (2009) Deep shade alters the acclimation response to moderate water stress in *Quercus Suber* L. Forestry 82(3):285–298

Kim Y-S, Chang C-S, Kim C-S, Gardner M (2011) The IUCN red list of threatened species 2011: e.T31244A9618913. 18 January 2017

Knapp AK, Hoover DL, Wilcox KR, Avolio ML, Koerner SE, La Pierre KJ, Loik ME, Luo Y, Sala OE, Smith MD (2015) Characterizing differences in precipitation regimes of extreme wet and dry years: implications for climate change experiments. Glob Change Biol 21:2624–2633

Kwon MY, Woo SY (2016) Plants' responses to drought and shade environments. Afr J Biotechnol 15:29–31

Lee B, Nam G, Yun J, Cho GY, Lee JS, Kim J, Park TS, Kim K, Oh K (2010) Biological indicators to monitor responses against climate change in Korea. Korean J Plant Taxon 40:202–207

Lepeduš H, Begović L, MlinarIć S, Šimić D, Štolfa I, Parađiković N, Užarević Z, Jurković V, Cesar V (2011) Physiology and biochemistry of leaf bleaching in prematurely aging maple (*Acer saccharinum* L.) trees. II. Functional and molecular adjustment of PSII. Acta Bot Croat 70:133–146

Li L, Zhou Z, Liang J, Lv R (2015) In vivo evaluation of the high-irradiance effects on PSII activity in photosynthetic stems of *Hexinia polydichotoma*. Photosynthetica 53:621–624

Lichtenthaler HK, Ač A, Marek MK, Kalina J, Urban O (2007) Differences in pigment composition, photosynthetic rates and chlorophyll fluorescence images of sun and shade leaves of four tree species. Plant Physiol Biochem 45:577–588

Lim J, Woo S, Kwon M, Kim Y (2007) Antioxidant enzyme activities and soil properties of healthy and declining *Abies koreana* (Wils.) in Mt. Halla. J Korean For Soc 96(1):14–20

Matsubara S, Chow WS (2004) Populations of photoinactivated photosystem II reaction centers characterized by chlorophyll a fluorescence lifetime in vivo. Proc Natl Acad Sci USA 101:18234–18239

Medrano H, Escalona JM, Bota J, Gulías J, Flexas J (2002) Regulation of photosynthesis of C3 plants in response to progressive drought: stomatal conductance as a reference parameter. Ann Bot 89(7):895–905

Murchie EH, Horton P (1997) Acclimation of photosynthesis to irradiance and spectral quality in British plant species: chlorophyll content, photosynthetic capacity and habitat preference. Plant Cell Environ 20:438–448

Nobel SP (2009) Photochemistry of photosynthesis—other photosynthetic pigments. Physicochemical and environmental plant physiology, 4th edn. Academic Press, Oxford, pp 238–244

Oguchi R, Terashima I, Kou J, Chow WS (2011) Operation of dual mechanisms that both lead to photoinactivation of Photosystem II in leaves by visible light. Physiol Plant 142:47–55

Oukarroum A, El Madidi S, Schansker G, Strasser RJ (2007) Probing the responses of barley cultivars (*Hordeum vulgare* L.) by chlorophyll a fluorescence OLKJIP under drought stress and re-watering. Environ Exp Bot 60:438–446

Pearcy RW, Sims DA (1994) Photosynthetic acclimation to changing light environments: scaling from the leaf to the whole plant. In: Caldwell MM, Pearcy RW (eds) Exploitation of environmental heterogeneity by plants: ecophysiological processes above and below ground. Academic Press, San Diego, pp 145–174

Powles SB (1984) Photoinhibition of photosynthesis induced by visible light. Ann Rev Plant Physiol 35:15–44

Rathod D, Brestic M, Shao H (2011) Chlorophyll a fluorescence determines the drought resistance capabilities in two varieties of mycorrhized and non-mycorrhized Glycine max Linn. African J Microbiol Res 5:4197–4206

Rodriguez-Dominguez CM, Buckley TN, Egea G, Cires A, Hernandez-Santana V, Martorell S, Diaz-Espejo A (2016) Most stomatal closure in woody species under moderate drought can be explained by stomatal responses to leaf turgor. Plant Cell Environ 39:2014–2026

Sancho-Knapik D, Peguero-Pina JJ, Flexas J, Herbette S, Cochard H, Niinemets Ü, Gil-Pelegrín E (2014) Coping with low light under high atmospheric dryness: shade acclimation in a Mediterranean conifer (*Abies pinsapo* Boiss.). Tree Physiol 34:1321–1333

Santabarbara S, Bordignon E, Jennings RC, Carbonera D (2002) Chlorophyll triplet states associated with photosystem II of thylakoids. Biochemistry 41(25):8184–8194

Sarijeva G, Knapp M, Lichtenthaler HK (2007) Differences in photosynthetic activity, chlorophyll and carotenoid levels, and in chlorophyll fluorescence parameters in green sun and shade leaves of Ginkgo and Fagus. J Plant Physiol 164:950–955

Schansker G, Tóth SZ, Strasser RJ (2005) Methylviologen and dibromothymoquinone treatments of pea leaves reveal the role of photosystem I in the Chl a fluorescence rise OJIP. Biochim Biophys Acta Bioenerg 1706:250–261

Schrader JA, Graves WR, Rice SA, Gibson JP (2006) Difference in shade tolerance help explain varying success of two synpatric *Alnus* L. species. Int J Plant Sci 5:979–989

Shao R, Wang K, Shangguan Z (2010) Cytokinin-induced photosynthetic adaptability of *Zea mays* L. to drought stress associated with nitric oxide signal: probed by ESR spectroscopy and fast OJIP fluorescence rise. J Plant Physiol 167:472–479

Smith JM, Paritsis J, Veblen TT, Chapman TB (2015) Permanent forest plots show accelerating tree mortality in subalpine forests of the Colorado Front Range from 1982 to 2013. For Ecol Manag 341:8–17

Stirbet A (2011) On the relation between the Kautsky effect (chlorophyll a fluorescence induction) and Photosystem II: Basics and applications of the OJIP fluorescence transient. J Photochem Photobiol B 104:236–257

Strasser RJ, Tsimilli-Michael M, Srivastava A (2004) Analysis of the chlorophyll a fluorescence transient. In: Papageorgiou GC, Govindjee (eds) Chlorophyll a fluorescence. Advances in photosynthesis and respiration, vol 19. Springer, Dordrecht, pp 321–362

Terashima I, Handa YT, Tholen D, Niinemets Ű (2011) Leaf functional anatomy in relation to photosynthesis. Plant Physiol 155(1):108–116

Valladares F, Niinemets U (2006) Shade tolerance, a key plant feature of complex nature and consequences. Annu Rev Ecol Evol Syst 39:237–257

Valladares F, Wright SJ, Lasso E, Kitajima K, Pearcy RW (2000) Plastic phenotypic response to light of 16 congeneric shrubs from a Panamanian rainforest. Ecology 81:1925–1936

Valladares F, Laanisto L, Niinemets Ü, Zavala MA (2016) Shedding light on shade: ecological perspectives of understorey plant life. Plant Ecol Diver 9:237–251

van Rensburg L, Krüger GH, Eggenberg P, Strasser RJ (1996) Can screening criteria for drought resistance in *Nicotiana tabacum* L. be derived from the polyphasic rise of the chlorophyll a fluorescence transient (OJIP)? S Afr J Bot 62(6):337–341

Vass I, Cser K (2009) Janus-faced charge recombinations in photosystem II photoinhibition. Trends Plant Sci 14(4):200–205

Vogelmann TC, Gorton HL (2014) Leaf: light capture in the photosynthetic organ. The structural basis of biological energy generation. Springer, Dordrecht, pp 363–377

von Caemmerer S, Farquhar G (1981) Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. Planta 153:376–387

Wagner A, McGraw JB (2013) Sunfleck effects on physiology, growth, and local demography of American ginseng (*Panax quinquefolius* L.). Forest Ecol Manag 291:220–227

Wang Z, Chen L, Ai J, Qin H, Liu Y, Xu P, Jiao Z, Zhao Y, Zhang Q (2012) Photosynthesis and activity of photosystem II in response to drought stress in Amur Grape (*Vitis amurensis* Rupr.). Photosynthetica 50:189–196

Wellburn AR, Lichtenthaler H (1984) Formulae and program to determine total carotenoids and chlorophylls a and b of leaf extracts in different solvents. In: Sybesma C (ed) Advances in photosynthesis research. Advances in agricultural biotechnology, vol 2. Springer, Dordrecht, pp 9–12

Woo SY, Lim J, Lee DK (2008) Effects of temperature on photosynthetic rates in Korean fir (*Abies koreana*) between healthy and dieback population. J Integr Plant Biol 50:190–193

Wyka T, Robakowski P, Żytowiak R (2008) Leaf age as a factor in anatomical and physiological acclimative responses of *Taxus baccata* L. needles to contrasting irradiance environments. Photosynth Res 95:87–99

Xu Z, Zhou G, Shimizu H (2010) Plant responses to drought and rewatering. Plant Signal Behav 5:649–654

Yamazaki JY, Suzuki T, Maruta E, Kamimura Y (2005) The stoichiometry and antenna size of the two photosystems in marine green algae, *Bryopsis maxima* L. and *Ulva pertusa* L., in relation to the light environment of their natural habitat. J Exp Bot 416:1517–1523