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BRIEF COMMUNICATION

Combined stresses of light and chilling on photosynthesis of *Fraxinus mandschurica* seedlings in northeastern China

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Abstract

The chilling and light stresses were experimentally created to explore photosynthesis of *Fraxinus mandshurica* seedlings in northeast China. Net photosynthetic rate, stomatal conductance, and transpiration rate decreased significantly with the decline of temperature and light. Significant interaction effects of light and chilling were observed on gas exchange of photosynthesis. The minimal fluorescence yield of the dark-adapted state (F_0) increased with increasing light and decreasing temperature. Both high and low light stresses induced the decreases of the maximal quantum yield of PSII photochemistry (F_v/F_m), photochemical quenching coefficient (q_P), nonphotochemical quenching (NPQ), and electron transport rate. Decline of F_v/F_m and increased F_0 were observed under decreasing temperatures. Decreased NPQ and q_P at frost temperature suggest that *F. mandschurica* failed to dissipate excess light energy. No interactive effects of chilling and light on chlorophyll fluorescence parameters suggests that *F. mandschurica* seedlings might be adapted to combined stresses of light and chilling.

Additional key words: chlorophyll fluorescence; early-spring chilling; net photosynthetic rate; temperate zone.

Plant growth is continuously influenced by various environmental conditions (Macedo *et al.* 2011, Yang *et al.* 2016a,b, Hu *et al.* 2017). Among those, temperature and light have been regarded as two prominent factors imposing great impacts on plant growth and photosynthesis (Riikonen *et al.* 2016, Guo *et al.* 2016). In the natural environments, low or high temperatures usually influence negatively plant photosynthesis (Zinn *et al.* 2010, Rahman 2013). As a primary source of energy for carbon fixation, light has also been thought to be one of the main factors affecting photosynthesis and causing photoinhibition of PSII (Fukuda *et al.* 2008, Weng *et al.* 2013).

Plants may suffer lethal stress symptoms under suboptimal or stressful temperatures (Allen and Ort 2001, Wingler 2015). Low temperature appears to be one of the most important factors that limit the growth and distribution of plants (Sonoike 2011). Although high temperatures cause damage of photochemical reactions in the chloroplasts (Yamori *et al.* 2008), chilling temperature is the most decisive factors that affect survival, growth, and reproduction of plants (Huang *et al.* 2010, Allen and Ort 2011, Bekele *et al.* 2014). Long-term exposures of chilling-sensitive plants to low temperatures often result in photoinhibition and oxygen-dependent bleaching of chlorophyll (Chl) pigments (Sonoike 1999, Lukatkin *et al.* 2012).

The negative impacts of light stress on photosynthesis have been known for a long time (Zinn *et al.* 2010). Combined with temperature, light usually plays an important role in plant growth, morphogenesis, and other physiological responses (Ali *et al.* 2005, Fukuda *et al.* 2008, Li and Kubota 2009, Zinn *et al.* 2010). Low or high light intensity usually causes negative effects on Chl

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Abbreviations: Chl – chlorophyll; C_i – intercellular CO_2 concentration; E – transpiration rate; ETR – electron transport rate; F_0 – minimal fluorescence yield of the dark-adapted state; F_m – maximal fluorescence yield of the dark-adapted state; F_s – stable fluorescence; F_m' – maximum fluorescence in the light-adapted state; F_0' – initial fluorescence in the light-adapted state; F_v/F_m – maximal quantum yield of PSII photochemistry; g_s – stomatal conductance; NPQ – nonphotochemical quenching; P_N – net photosynthetic rates; q_P – photochemical quenching coefficient.

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content, ultrastructure of photosynthetic apparatus, gas exchange of leaves, enzyme activities, as well as physiological and photochemical processes (Bailey *et al.* 2001, Sonoike 2011, Yang *et al.* 2016a,b). Low light intensity may decrease net photosynthetic rates (P_N) of plants and reduce their growth (Huang *et al.* 2011, Dong *et al.* 2014).

The stresses of light and temperature on plants usually interact under natural conditions (Kudoh and Sonoike 2002). At low temperatures, excessive light is expected to further decrease photosynthetic capacity (Baker 1994). Although previous studies mainly focused on the impacts of either light intensity or temperature on plants (Allen and Ort 2011, Li *et al.* 2016, Pettigrew 2016, Riikonen *et al.* 2016), little is known about their combined effects on the growth and photosynthesis of woody plants (Štroch *et al.* 2010). Moreover, most experiments were carried out with tropical species that are not acclimatized to stressful environments (Huang *et al.* 2010, 2012; Allen and Ort 2011, Hou *et al.* 2016).

In the deciduous broad-leaved forests in northeastern China, one-year seedlings and new sprouts of trees are usually subjected to early-spring chilling stress combined with varying light intensities. Low temperature throughout the night and the consequent high light irradiance after sun rising are supposed to be interactive stresses to plants in this area. However, it remains to be answered how the chilling temperatures interact with light intensities to affect plant growth and photosynthesis and how these plants acclimatize to the stressful environments. *Fraxinus mandshurica* is a native hardwood tree species widely distributed in northeast China, Japan, Korea, and eastern Russia (Kong *et al.* 2012). In the present study, we artificially created different irradiance intensities under chilling temperature around zero, in order to explore the responses of photosynthesis in *Fraxinus mandshurica* seedlings to the combined stresses of chilling temperature and light in northeast China.

Seeds were planted in Qingyuan Forest CERN (Zhu *et al.* 2007), Chinese Academy of Sciences. One-year seedlings (about 8–12 cm in height and 6–8 leaves) of *F. mandshurica* were collected and immediately transferred into plastic pots (11 × 8.5 × 9.5 cm) for experiments in 2015. After 20-d acclimation, which is presumed to be enough for recovery from initial transplanting based on leaf color, the seedlings were transferred into constant temperature incubator (*ET-010L*, *Espec*, Shanghai, China) and subjected to chilling and light treatments according to the ambient temperatures and light irradiations in the early spring at Qingyuan Forest CERN (Zhu *et al.* 2007). The initial temperature for all seedlings was set at 10°C and then decreased to 4, 2, 0, and –2°C at a speed of 2°C h^{-1}, in order to create four levels of chilling treatments. Each chilling treatment in our study contained 15 seedlings. After 8-h incubation at different temperatures, the seedlings under each chilling treatment were randomly divided into three identical groups and transferred to room temperature of 20°C and immediately illuminated with three different levels of white light [L1: 1,200 μmol (photon) m^{-2} s^{-1}, L2: 500 μmol(photon) m^{-2} s^{-1}, and L3: 80 μmol(photon) m^{-2} s^{-1}] for 3 h. Our chilling and light treatments on *F. mandshurica* seedlings simulated the low temperature at night and following light irradiance in the morning in the study area.

Then, net photosynthetic rates (P_N), intercellular CO_2 concentration (C_i), transpiration rate (E), and stomatal conductance (g_s) were measured out of the laboratory with the fully expanded leaves using a *Li-6400* portable photosynthesis system (*Li-Cor*, Lincoln, NE, USA) during 8:30 to 12:00 h in sunny days. A total of 10 fully expanded leaves from the five seedlings of each group were randomly selected for measurements under ambient light and CO_2 concentration.

The Chl *a* fluorescence of PSII was measured by using a *FMS-2* fluorometer (*Hansatech*, England). A total of six leaves from the five seedlings were randomly selected for measurement of Chl fluorescence. Before each measurement, leaves were dark-adapted for 30 min. The minimal fluorescence yield of the dark-adapted state (F_0) was measured under a weak measuring light of modulating radiation (wavelength of 594 nm; pulse width of 1.8 ms), and maximal fluorescence yield of the dark-adapted state (F_m) was induced by a saturating white light [> 3,500 μmol(photon) m^{-2} s^{-1}; pulse width of 0.7 s] applied over constant 2.5 s for all experiments. An actinic white light source (the same as the treatment light) was then applied for 10 min to measure stable fluorescence (F_s). After that, a second white light (pulse width of 0.7 s) was applied for 2.5 s to obtain maximum fluorescence in the light-adapted state (F_m'). The initial fluorescence in the light-adapted state (F_0') was determined after switching off the actinic light and simultaneously applying 3 s of far red light (wavelength of 735 nm; pulse width, 1.8 ms). Maximal quantum yield of PSII photochemistry (F_v/F_m), photochemical quenching coefficient (q_P), and nonphotochemical quenching (NPQ) were calculated according to the methods proposed by Krause and Weis (1991): $F_v = F_m - F_0$, $q_P = (F_m' - F_s)/(F_m' - F_0')$, $NPQ = (F_m - F_m')/F_m$.

A two-way analysis of variance (*ANOVA*) was performed for each variable using *SPSS 16.0*, with temperature and light as the main fixed factor. Least significant difference (LSD) was used to compare the mean values of the levels of light and temperature treatments. Data were checked for normality and homogeneity of variance to satisfy the assumptions of *ANOVA*.

Two-way *ANOVA* analysis indicated that both P_N and E of *F. mandshurica* seedlings maintained higher at high and medium light irradiance ($F = 25.001$, df = 2, $P<0.001$; $F = 137.213$, df = 2, $P<0.001$) (Table 1). The lowest g_s was observed at light irradiance of 80 μmol(photon) m^{-2} s^{-1} ($F = 129.592$, df = 2, $P<0.001$) (Table 1). Two-way *ANOVA* analysis indicated that C_i increased significantly with the decrease of light intensity ($F = 74.269$, df = 2, $P<0.001$).

Table 1. Interactive effects of chilling and light stresses on net photosynthetic rates (P_N), stomatal conductance (g_s), intercellular CO_2 concentration (C_i), and transpiration rate (E) of *Fraxinus mandshurica* seedlings. L1, L2, and L3 – light intensities at 1,200; 500, and 80 µmol(photon) m^{-2} s^{-1}, respectively. $n = 10$. Data are expressed as mean ± SD. Different *lowercase letters* in the same column indicate significance at $P<0.05$, while different *uppercase letters* in the same row indicate significance at $P<0.05$.

Parameter	Light intensity	Temperature [°C]				
		4	2	0	-2	Mean
P_N [µmol m^{-2} s^{-1}]	L1	4.59 ± 0.40^{aA}	2.04 ± 0.79^{bA}	0.43 ± 0.16^{cA}	0.33 ± 0.21^{cA}	1.85
	L2	2.24 ± 1.04^{aB}	2.67 ± 0.34^{aA}	1.56 ± 0.76^{bB}	0.55 ± 0.11^{cA}	1.76
	L3	1.60 ± 0.32^{aB}	0.79 ± 0.16^{bB}	1.33 ± 0.44^{aB}	-0.01 ± 0.07^{cB}	0.93
	Mean	2.81	1.83	1.11	0.30	-
g_s [mmol m^{-2} s^{-1}]	L1	0.03 ± 0.002^{aA}	0.03 ± 0.01^{aA}	0.02 ± 0.001^{bA}	0.01 ± 0.002^{cA}	0.02
	L2	0.03 ± 0.001^{aA}	0.03 ± 0.002^{aA}	0.02 ± 0.002^{bA}	0.01 ± 0.001^{cA}	0.02
	L3	0.01 ± 0.001^{aB}	0.02 ± 0.004^{bB}	0.01 ± 0.004^{aB}	0.01 ± 0.001^{aA}	0.01
	Mean	0.02	0.03	0.02	0.01	-
C_i [µmol mol^{-1}]	L1	215.6 ± 2.1^{aA}	223.6 ± 1.8^{bA}	251.0 ± 2.9^{cA}	293.9 ± 10.4^{dA}	246
	L2	226.6 ± 2.6^{aB}	232.6 ± 8.6^{bB}	237.5 ± 11.6^{bA}	269.2 ± 8.0^{cB}	241.5
	L3	225.4 ± 10.0^{aB}	262.9 ± 0.8^{bC}	282.6 ± 8.8^{cB}	345.3 ± 24.2^{dC}	279
	Mean	222.5	239.7	257	302.8	-
E [mmol m^{-2} s^{-1}]	L1	1.25 ± 0.27^{aA}	0.59 ± 0.04^{bA}	0.51 ± 0.01^{bA}	0.17 ± 0.02^{cA}	0.63
	L2	0.90 ± 0.05^{aB}	0.94 ± 0.11^{aB}	0.84 ± 0.13^{bB}	0.17 ± 0.02^{cA}	0.71
	L3	0.27 ± 0.01^{aC}	0.38 ± 0.02^{bC}	0.39 ± 0.04^{bC}	0.17 ± 0.01^{aA}	0.30
	Mean	0.81	0.64	0.58	0.17	-

Both P_N and E decreased significantly with the decline of chilling temperatures ($F = 92.861$, df = 3, $P<0.001$; $F = 153.595$, df = 3, $P<0.001$) (Table 1). The g_s maintained the highest values at 2°C ($F = 303.806$, df = 3, $P<0.001$), while C_i increased significantly with the decrease of temperatures ($F = 179.191$, df = 3, $P<0.001$). Significant interactive effects of light and chilling temperature were observed on P_N ($F = 25.421$, df = 6, $P=0.002$), g_s ($F = 39.631$, df = 6, $P<0.001$), C_i ($F = 9.926$, df = 6, $P< 0.001$), and E ($F = 49.585$, df = 6, $P<0.001$) (Table 1).

F_0 remained at the highest level at irradiance of 1,200 µmol(photon) m^{-2} s^{-1} ($F = 22.545$, df = 2, $P<0.001$) (Fig. 1*A*). F_v/F_m maintained the highest value at medium light irradiance intensities ($F = 34.950$, df = 2, $P<0.001$). With the decrease of temperatures, deceased F_0 ($F = 14.846$, df = 3, $P<0.001$), but increased F_v/F_m ($F = 13.095$, df = 3, $P<0.001$) were observed (Fig. 1*A*,*B*). NPQ (light: $F = 21.819$, df = 2, $P<0.001$; temperature: $F = 20.474$, df = 3, $P<0.001$), q_P (light: $F = 29.381$, df = 2, $P<0.001$; temperature: $F = 10.683$, df = 3, $P<0.001$), and ETR (light: $F = 11.561$, df = 2, $P<0.001$; temperature: $F = 14.133$, df = 3, $P<0.001$) showed similar patterns to F_v/F_m under different light and chilling-temperature treatments (Fig. 1*C*–*E*). Based on two-way *ANOVA* analysis, we detected no significant interactive effects of light and temperature on F_0, F_v/F_m, q_P, NPQ, and ETR.

Our results showed that chilling temperatures showed substantial negative impacts on gas-exchange parameters of *F. mandschurica* (Table 1), in agreement with the previous studies on the effects of chilling stress (Allen and Ort 2001, Sonoike 2011, Hou *et al.* 2016). Despite wide distribution in the temperate zone in northeast China, photosynthetic processes (*e.g.,* P_N) of *F. mandschurica* seedlings were very sensitive to low temperatures. Photosynthetic enzymes (*e.g.,* Rubisco) may be inactivated or even degraded when plants are exposed to chilling stresses, resulting in a decrease of photosynthetic activity of *F. mandschurica*. Moreover, P_N, g_s, and E decreased significantly with the decline of light intensities (Table 1), indicating the important role of irradiance on photosynthesis (Dong *et al.* 2014). Maintaining high level of P_N at 1200 µmol(photon) m^{-2} s^{-1} implies that seedlings of *F. mandschurica* may possess a high light-saturation point (LSP). However, C_i increased with the decreasing light intensities and chilling temperatures (Table 1), possibly due to the downregulation of photosynthesis and carbon assimilation capacity (Hou *et al.* 2016). Although high light promoted P_N of *F. mandschurica* at 4°C, the negative effect of low temperature on photosynthesis was more pronounced when combined with a low irradiance (Huang *et al.* 2010). Compared to light stress, low temperature appeared to show greater influences on photosynthesis of *F. mandschurica*, reflecting that chilling is one of the most important stress factors. P_N depends not only on photosynthesis but also on respiration (Krause and Weis 1991). Therefore, changes in P_N of *F. mandschurica* seedlings under light and chilling treatments can also be explained partially by the variations in respiration rates, which are usually enhanced at high light and temperatures (Guo *et al.* 2015).

F_0 of *F. mandschurica* seedlings exhibited significant increases either with increasing light intensity or

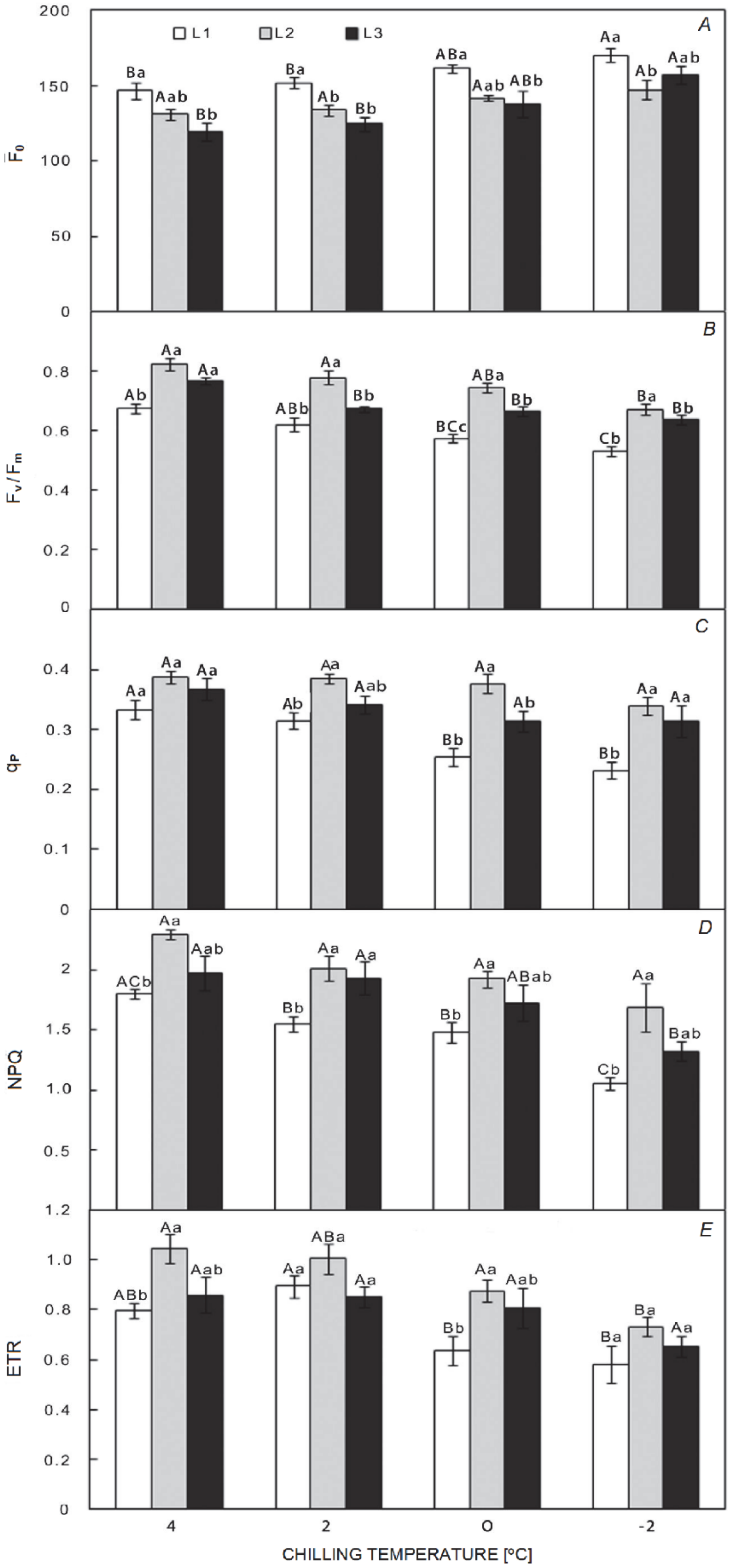

Fig. 1. The effects of temperature and light stresses on the minimal fluorescence yield of the dark-adapted state (F_0), maximal quantum yield of PSII photochemistry (F_v/F_m), photochemical quenching coefficient (q_P), nonphotochemical quenching (NPQ), and electron transport rate (ETR) of *Fraxinus mandshurica* seedlings. L1, L2, and L3 refer to light intensities at 1,200, 500, and 80 µmol(photon) m^{-2} s^{-1}, respectively. $n = 6$ for all measurements. Data are expressed as mean ± SE. Different *lowercase letters* indicate significance among light treatments at $P<0.05$ level, while different *uppercase letters* indicate significant changes among chilling treatments at $P<0.05$ level.

decreasing temperature (Fig. 1*A*). The increase in F_0 of *F. mandschurica* can be attributed to the disconnection of the inner antennae and light-harvesting complex from the core of PSII, or to the release of free Chl from protein-pigment complex (Briantais *et al.* 1996), or the changing microenvironment of the Chl in thylakoids during the phase transition for bulk lipids (Krumova *et al.* 2010, Tovuu *et al.* 2013). Both high and low light stresses [80 and 1200 μmol(photon) m^{-2} s^{-1}] decreased F_v/F_m, NPQ, q_P, and ETR compared to the medium light irradiation at 500 μmol(photon) m^{-2} s^{-1} (Fig. 1*B*,*C*,*D*). High light at the early spring may promote photosynthesis, but may also show negative impacts on photochemical processes of *F. mandschurica*. Significant decreases in F_v/F_m and increased F_0 were observed in response to chilling temperatures (Fig. 1*A*,*B*), possibly indicating photoinhibition of PSII of *F. mandschurica* under suboptimal light intensities (Krause *et al.* 1995, Yoshida *et al.* 2007), because damage to PSII is often the first manifestation of stress in a leaf (Mathur *et al.* 2011). Chilling stress significantly decreased all the Chl fluorescence parameters, verifying the facts that plants subjected to chilling and high light often show significant photoinhibition (Lamontagne *et al.* 2000). The decrease of NPQ and q_P at frost temperatures suggests that *F. mandschurica* is unable to effectively dissipate excess light energy in the chloroplasts (Huang *et al.* 2012). The higher values of NPQ, q_P, and ETR at 4°C may represent photoprotection mechanisms (*e.g.*, heat dissipation) in the chloroplasts of *F. mandschurica*, to prevent photoinhibition at high irradiance (Ort and Baker 2002). Although photoinhibition increases nonlinearly with decreasing temperature and linearly with increasing light intensity (Hetherington *et al.* 1989), we detected no significant interactive effects of chilling and light on the Chl fluorescence parameters, inconsistent with the previous study (Hu *et al.* 2010). These observations suggest that seedlings of *F. mandschurica* may be adapted to the combined stresses of light and chilling at the early stage in the spring.

Our results showed that stresses of chilling and light impose substantial impacts on seedlings of *F. mandschurica*. Both high and low light irradiance showed negative effects on gas exchange of *F. mandschurica*, suggesting a moderate light intensity may support seedling growth of *F. mandschurica*, especially at the early stage of development. Our study may provide insight into understanding plant photosynthesis under combined chilling and light intensity stress in temperate areas. Although gas exchange was significantly reduced by chilling and light treatments, seedlings of *F. mandschurica* were more susceptible to chilling stress than to that of high light intensity (Table 1). Therefore, we suggest that protection from chilling injury at the early stage may be beneficial for growth and survival of *F. mandschurica* seedlings in the study areas.

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