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SHORT COMMUNICATION

Mild abiotic stresses have different effects on chlorophyll fluorescence parameters in leaves of young woody and herbaceous invasive plants

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Abstract The effects of abiotic stresses (high and chilling temperatures, and drought) on woody (*Acer negundo* L., *Fraxinus pennsylvanica* Marsh.), and herbaceous [*Conysa canadensis* L., *Echinocystis lobata* (Michx.) Torr. et Gray] invasive plants have been assessed by establishing chlorophyll fluorescence (ChlF) indexes for the leaves of seedlings. Our data indicate that the four invasive plants have different mechanisms in place to change ChlF in response to high or low temperature, or drought. In particular, we noted that photochemical quenching of ChlF was depressed (except for *F. pennsylvanica* during chilling) while non-photochemical quenching of ChlF was activated in woody plants (except for drought) in response to these stresses. This effect, which was related to the inhibition of PSII activity, allowed for partial reduction of the quinone pool. In contrast, enhanced PSII activity and suppressed non-photochemical quenching in the leaves of *C. canadensis* was observed in response only to high temperature stress. This may have resulted from an increase in the oxidation of the quinone pool, which helps to activate electron transport between the two photosystems. In addition, both herbaceous plants displayed high tolerance to drought when compared to *F. pennsylvanica*, a woody plant. These differences in the response of the photosynthetic apparatus to stresses may lie in differences in the adaptive ability of invasive species to secondary habitats.

Keywords Carotenoids · Drought · Fluorescence quenching · Low and high temperatures · PSII · Quinone pool

Abbreviations

AL	Actinic light
Car	Carotenoid
ChlF	Chlorophyll fluorescence
^{3}Cl*	Triplet state of chlorophyll
FR	Far-red light
F_v/F_m	Maximum quantum yield of PSII photochemistry
IC	Induction curve
ML	Measuring light
NPQ	Non-photochemical quenching
PAM	Pulse amplitude modulated
q_N	Non-photochemical quenching coefficient
q_P	Photochemical quenching coefficient
ROS	Reactive oxygen species
Φ_{PSII}	Effective quantum yield of PSII photochemistry
Y(NO)	Quantum yield of non-photochemical nonlight-induced quenching of ChlF
Y(NPQ)	Quantum yield of non-photochemical light-induced quenching of ChlF

Introduction

One aspect related to the conservation of plant biodiversity involves the control of alien species, which may influence the state of natural floral populations in the form of

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biological invasions. The spread of invasive plants is increasing and has become a global ecological problem (McGeoch et al. 2016). The physiological mechanisms that invasive species employ to adapt to secondary habitats increase their ability to survive (Skalová et al. 2015). One of the mechanisms that invasive species has is high tolerance to abiotic and anthropogenic stresses (Souza et al. 2011) which allows invasive plants to withstand competition from native species, and even show higher adaptive capacity, thus reducing the diversity of native plants (Alba and Hufbauer 2012; Künzi et al. 2015). Temperature and nutrients strongly affect the growth and development of seedlings of invasive plants (Skalová et al. 2015).

One method to assess a plant's tolerance to stresses is by determining ChlF (Sayed 2003). The physiological state of the photosynthetic apparatus is highly sensitive to different stresses and is thus considered to be an extremely reliable method for assessing the tolerance of plants to stresses. ChlF is a physical phenomenon and a known reliable indicator of the photosynthetic apparatus activity of higher plants (Strasser et al. 1998; Zaks et al. 2013). This helpful indicator has been used to research the effect of variable abiotic stresses (e.g., high, low, and freezing temperatures; drought) on the photosynthetic apparatus (Sayed 2003), chloroplasts, and photosynthetic membranes (Khurana et al. 2015). Up to 98% of ChlF is emitted by components of photosystem II (PSII), and a change in the output of ChlF can be considered to reflect the effectiveness of photochemical reactions, including direct effects on the separation of charges ($P680^{+}$ $Pheo^{-}$), the rate of electron transport (Johnson et al. 2014), the size and redox state of the quinone pool (Wilson and Huner 2000), and the dissipation and accumulation of light energy (Kramer et al. 2004; Zaks et al. 2013; Zhou et al. 2015). The main ChlF indices that are used as stress-tolerance indicators are F_v/F_m, q_P, q_N, and Φ_{PSII}, all of which have been used to show different reactions of the photosynthetic apparatus to environmental stresses (Strasser et al. 1998; Zaks et al. 2013).

A wide range of stress factors can negatively affect or suppress vital processes in plants, and the level of damage was assessed by ChlF-related parameters, including water deficit (Sayed 2003; Castillo et al. 2007; Molina-Montenegro et al. 2010; Khurana et al. 2015), salt stress (Sayed 2003; Castillo et al. 2005; Khurana et al. 2015), and extreme temperatures, namely freezing (Griffith et al. 2014), chilling temperatures (Sayed 2003), and heat stress (Khurana et al. 2015).

In this study, we attempted to reveal the tolerance of young invasive plant species to abiotic stresses that can restrict their wide dissemination at early developmental stages, which are most critical for survival. Moreover, we show that this tolerance can be estimated from changes in the functioning of the photosynthetic apparatus, which can be detected by ChlF. We compared the degree of tolerance of four plant species (two herbaceous and two woody plants) to three abiotic stresses in a bid to explain the physiological mechanisms related to the functioning of the photosynthetic apparatus and that form the basis of their tolerance to abiotic stresses. In temperate zones such as central Russia, young plantlets are affected by chilling or high temperatures, and by water deficit stress which, even in a mild form, have a damaging effect on the growth and development of plants (Krasensky and Jonak 2012).

Even though many studies have used ChlF as the main index to assess the tolerance of invasive plants to the environment, it is not known whether this is a general property of all invasive plants. Moreover, it is unclear whether it is possible to use changes to ChlF indexes to assess the tolerance of plants to different stresses. In Central Russia, invasive species are extremely common, in particular *Acer negundo* L., *Fraxinus pennsylvanica* Marsh., *Conysa canadensis* L., and *Echinocystis lobata* (Michx.) Torr. et Gray, for which no data on the impact of abiotic stresses on the state of the photosynthetic apparatus exists. *Acer negundo* grows over a wide area of Russia and Europe, after being introduced into the native flora, and breed successfully (Saccone et al. 2010), being assimilated into many anthropogenic and natural habitats and displacing several native species (Erfmeier et al. 2011). *Fraxinus pennsylvanica* is widely cultivated in the southern latitudes of Europe and Russia and is a highly invasive species while its dispersal at northern latitudes is more restricted to cities (Kremer et al. 2006). *Conysa canadensis* is found in natural habitats where it competes with agricultural crops for nutrients (Har-Edom and Sternberg 2010). *Echinocystis lobata*, which is widely found in Russia's floodplains where it forms extensive thickets in coastal scrubland, grows rapidly, and its large vegetative mass may displace more photophilic plants, creating unfavorable conditions for them (Olonova and Zhang 2013). Therefore, the aim of this study was to evaluate in seedlings, using ChlF measurements, the tolerance of these four invasive plant species—two of which are woody and the other two herbaceous—to drought and extreme temperature stress.

Materials and methods

Two woody plants, American maple (*A. negundo*) and Pennsylvania ash (*F. pennsylvanica*), and two herbaceous plants, Canadian horseweed (*C. canadensis*) and wild cucumber (*E. lobata*), were selected for this study due to their invasiveness and high abundance in temperate areas of Eurasia.

Seeds were collected from locations in Mordovia, Russia, where they grow naturally: *E. lobata* at 1 km north-northwest of the village Tashkino, Ichalkovsky district (54°44′166,280″N; 45°28′367,218″E); *A. negundo* and *E. canadensis* at 900 m south-southwest of the village Haji, Lyambirsky district (54°19′37,713″N; 45°14′442,430″E); *F. pennsylvanica* from Titova Str., Saransk (54°12′255,475″N; 45°9′588,109″E). Seed samples were collected from several plants (3–7) and then pooled for lab tests.

Plants were grown in the laboratory in pots with soil (degraded Chernoziom, 2 kg per vessel) for 45–60 days under cold fluorescent lamps (Philips TL-D 30/54-765, Poland) with PPFD of 50 μmol (photon) m^{-2} s^{-1} (12-h photoperiod), 80% relative humidity and at 25 °C. These experimental conditions were defined as most acceptable in preliminary experiments. Thermal stress was simulated by placing pots with seedlings for 6 h under conditions of high (40 °C) or low (5 °C) temperatures. To mimic water deficit conditions, seedlings were placed under the same growth conditions but without watering for 2 days. Control pots, as well as high/low temperature stress variants, were watered every day.

ChlF parameters in 2–3 mature leaves were determined by a portable fluorometer—Junior PAM (Heinz-Walz, Germany). Before registering ChlF induction curves (IC), 45–60 days-old seedlings were first placed in the dark for 60 min immediately after the stress. IC was recorded in the following conditions and was selected experimentally according to the design described in Fig. 1 (Pfündel 2007): PPFD of the measuring light (ML) 40 μmol (photon) m^{-2} s^{-1} (450 nm, 5 Hz); saturation pulse (SP) 1500 μmol (photons) m^{-2} s^{-1} (450 nm); actinic light (AL) 285 μmol (photons) m^{-2} s^{-1} (450 nm); far red light (FR) 1500 μmol (photon) m^{-2} s^{-1} (730 nm). The photochemical activity of PSII was assessed by calculating the following indicators: F_v/F_m, (Eq. 1) is maximal quantum yield of PSII photochemistry (Strasser et al. 1998); q_P, photochemical quenching coefficient (Eq. 2); q_N, non-photochemical quenching coefficient (Eq. 3); Φ_{PSII}, $Y(NPQ)$, $Y(NO)$, the effective photochemical quantum yields of PSII, as well as the non-photochemical light-induced and non-photochemical nonlight-induced quenching of ChlF (Eqs. 4–6), respectively (Kramer et al. 2004):

$$F_V/F_M = \frac{F_M - F_0}{F_M}, \tag{1}$$

$$q_P = \frac{F'_M - F'}{F'_M - F'_0}, \tag{2}$$

$$q_N = 1 - \frac{F'_M - F'_0}{F_M - F_0}, \tag{3}$$

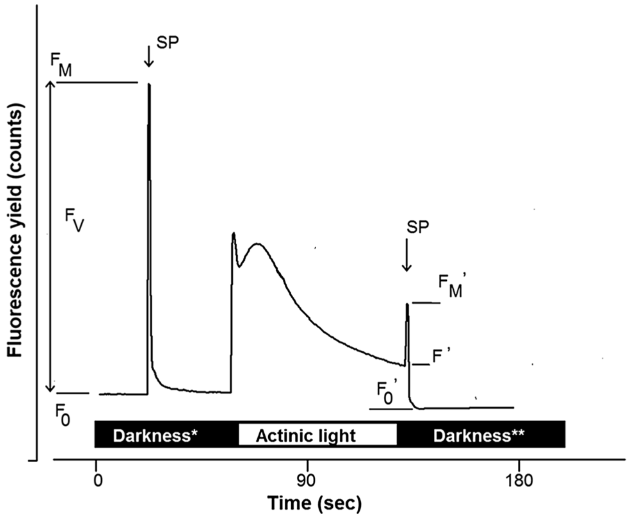

Fig. 1 Registration of induction curve of ChlF: *Darkness** measuring light; *SP* saturating pulse; *Darkness*** far-red illumination

$$Y(\mathrm{II}) = \frac{F'_M - F'}{F'_M}, \tag{4}$$

$$Y(\mathrm{NO}) = \frac{1}{\left(\frac{F_M}{F'_M} - 1\right) + 1 + q_p \times \frac{F'_0}{F'} \times \left(\frac{F_M}{F_0} - 1\right)}, \tag{5}$$

$$Y(\mathrm{NPQ}) = 1 - Y(\mathrm{II}) - Y(\mathrm{NO}), \tag{6}$$

where F_v = variable fluorescence level; F_0 = minimum fluorescence level excited by a very low intensity of measured light; in this condition, PSII reaction centers are open; F_M = maximum fluorescence level induced by SP, which closes all PSII reaction centers; F'_M = minimum fluorescence level during actinic light treatment; F'_M = -maximum fluorescence level during actinic light treatment that is induced by applying a SP which temporarily closes all PSII reactions centers; F' = the level of the fluorescence curve during an actinic light treatment and shortly before a SP is applied.

Three independent experiments were conducted, each with three replicates (separate plants from each treatment) with seven samples each. Averages and SE were calculated in Microsoft Excel 2000, Biostat, and Statistica version 2.6. Significant differences were assessed by Tukey's multiple range test at $P = 0.05$.

Results and discussion

The success of an invasive species may be due to higher values of tolerance to abiotic stresses and disturbed environment than native species. This study assessed the photochemical and non-photochemical quenching of ChlF in the leaves of two trees and two herbaceous species as affected by chilling, high temperature, and drought stress.

In the leaves of *F. pennsylvanica*, $\varPhi_{\mathrm{PSII}}$, q_{N}, q_{P}, Y(NPQ) and $F_{\mathrm{v}}/F_{\mathrm{m}}$ were reduced (relative to the control) by drought, and q_{P} and Y(NO) by high temperature (Figs. 2, 3, 4, 5, 6, 7). Y(NO) was also reduced by chilling. Conversely, q_{N} and Y(NPQ) were increased by high temperatures and chilling while Y(NO) was increased 95% by drought (Figs. 4, 5, 6). The reduction of ChlF indexes in the leaves of *F. pennsylvanica* by drought stress varied from 28 to 58%, but was maximum in $F_{\mathrm{v}}/F_{\mathrm{m}}$.

In the leaves of *A. negundo* (see Figs. 2, 3), $\varPhi_{\mathrm{PSII}}$ and q_{P} were reduced by drought, chilling, and high temperature while drought alone decreased $F_{\mathrm{v}}/F_{\mathrm{m}}$ by 8% (Fig. 7). Three indexes [$\varPhi_{\mathrm{PSII}}$, q_{P} and Y(NO)] decreased in response to high and chilling temperatures (Figs. 2, 3, 5). Conversely, Y(NPQ) was increased by the same stresses (Fig. 6), but mostly by high temperature (38% higher than the control).

In the two herbaceous plants exposed to stresses, we observed a somewhat different picture. In the leaves of *C. canadensis*, q_{N} was reduced only by drought (Fig. 4). Y(NPQ) and Y(NO) were reduced by high temperature (Figs. 5, 6), which increased $\varPhi_{\mathrm{PSII}}$ (Fig. 2) and q_{P} (Fig. 3) by 79 and 55%, respectively.

In the leaves of *E. lobata*, q_{P} and Y(NO) were reduced by chilling (Fig. 5), but q_{N} and Y(NPQ) were reduced by high temperature (see Figs. 4, 5). Conversely, Y(NPQ) increased in response to chilling and Y(NO) increased in response to high temperature.

We found that abiotic stresses might have a different impact on woody and herbaceous plants. In a woody plant (*F. pennsylvanica*), there was a decline in photo- and non-photochemical ChlF quenching [q_{P}, q_{N}, Y(NPQ)] by drought (Figs. 3, 4, 6). Simultaneously, the decrease in light and nonlight-induced losses in response to drought showed highest negative effects of this stress on plants and was associated with the degradation of the photosynthetic apparatus (especially in *F. pennsylvanica*). In a herbaceous plant (*C. canadensis*), electron transport between the two photosystems was activated by high temperature stress, reflected by an increase in oxidation of the quinone pool and effective quantum yield of PSII, with a simultaneous reduction of losses in NPQ [Y(NO), Y(NPQ)].

Thus, the effect of unfavorable temperatures led to the inhibition of photochemical quenching (except for *F. pennsylvanica* by chilling stress), and to activation of non-photochemical quenching ChlF in the leaves of woody plants but drought led to the highest negative effect. According to Allen and Ort (2001), the effect of low temperatures is accompanied by a decrease in the efficiency of the quantum yield of PSI and PSII, activation of ATP synthase and a reduction of stromal enzymes in the carbon cycle. Low temperatures increase the content of carotenoids (Cars), which protect against chlorophyll degradation (Reda and Mandoura 2011). An increase in Car content is related to over-recovery of the quinone pool (Wilson and Huner 2000) and may be a signal for the intensification of antioxidants production (Cars, tocopherols, ascorbic acid, etc.) because it increases the probability of ROS formation when the quinone pool is reduced (Allen and Ort 2001). When the probability of ROS formation increases, the content of ROS quenchers also increases (Wilson and Huner 2000). For instance, Cars production, especially xanthophylls, boosts the probability of ΔpH-dependent NPQ because xanthophylls play an active role in the disposal of excess light energy through mechanisms of violaxanthin- and lutein-epoxide-cycles (Jahns et al. 2009; Zhou et al. 2015).

It is likely that similar mechanisms take place in response to low and high temperatures in the case of woody plants. Heat stress inhibited the photochemical activity of PSII: a decrease in $\varPhi_{\mathrm{PSII}}$ (*A. negundo*) values indicates that high temperatures caused structural and functional injury of the antenna complexes (and probably PSII reaction centers); and partial reduction of the quinone pool in both woody plants. In the absence of an energy acceptor, for

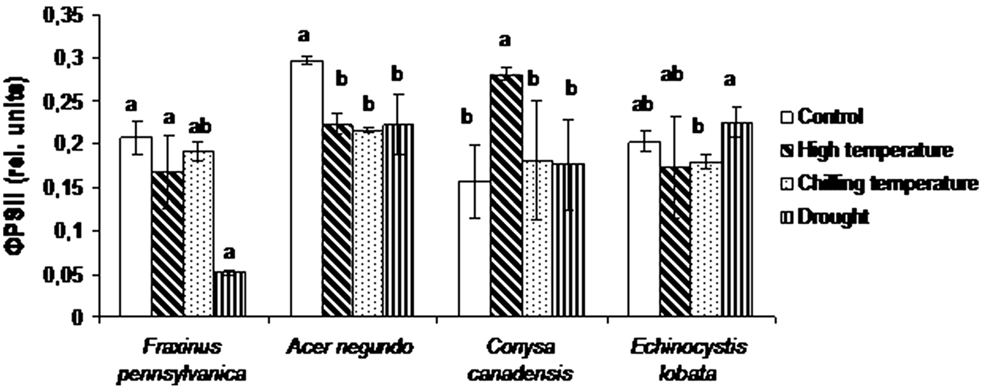

Fig. 2 The effective photochemical quantum yield of PSII from woody and herbaceous plants in response to abiotic stresses. *Different letters* within a species indicate significant differences between treatment means (Tukey's test; $P \leq 0.05$)

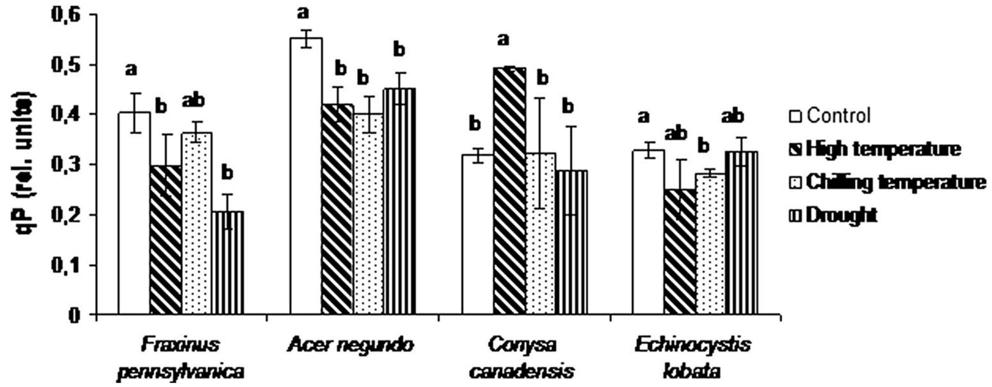

Fig. 3 The coefficient of photochemical quenching ChlF from woody and herbaceous plants in response to abiotic stresses. *Different letters* within a species indicate significant differences between treatment means (Tukey's test; $P \leq 0.05$)

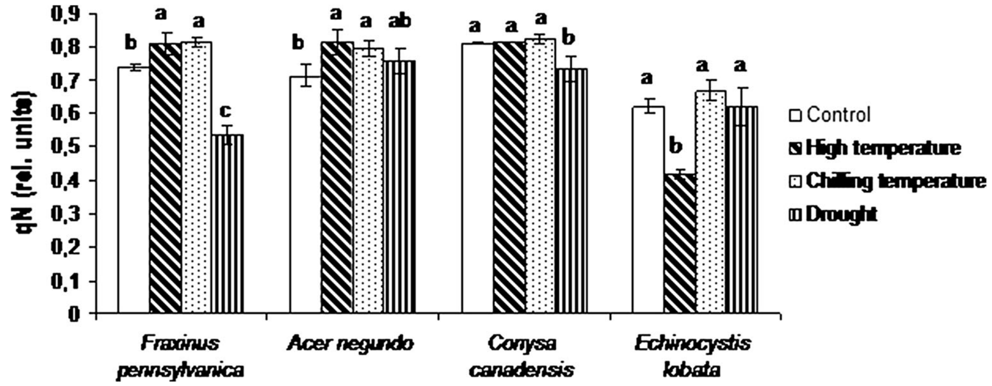

Fig. 4 The coefficient of non-photochemical quenching ChlF from woody and herbaceous plants in response to abiotic stresses. *Different letters* within a species indicate significant differences between treatment means (Tukey's test; $P \leq 0.05$)

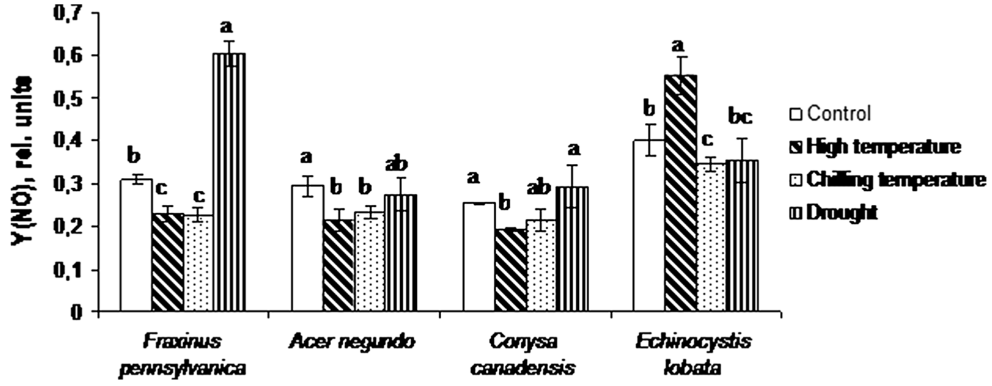

Fig. 5 The quantum yield of non-photochemical non-light-induced ChlF from woody and herbaceous plants in response to abiotic stresses. *Different letters* within a species indicate significant differences between treatment means (Tukey's test; $P \leq 0.05$)

example the quinone pool or xanthophylls, or a decrease in their content, the PSII antenna-absorbed excitation energy increases the probability of formation of chlorophyll triplet forms (^{3}Cl*), increasing the possibility of ROS formation (Krieger-Liszkay and Trebst 2006). Usually, in this case, the content of antioxidants and quenchers of ^{3}Chl* (tocopherols, carotenes, xanthophylls, etc.) increases and an increase in the content of xanthophylls (zeaxanthin, lutein) may have taken place, which would lead to an increase of *q*N through the photoprotective mechanism of energy dissipation (Jahns et al. 2009; Zhou et al. 2015). In turn, the possibilities to activate PSI and ATP synthase may be due to the "oppression" of electron transport between the two photosystems (PSII and b6f-complex) which can cause the

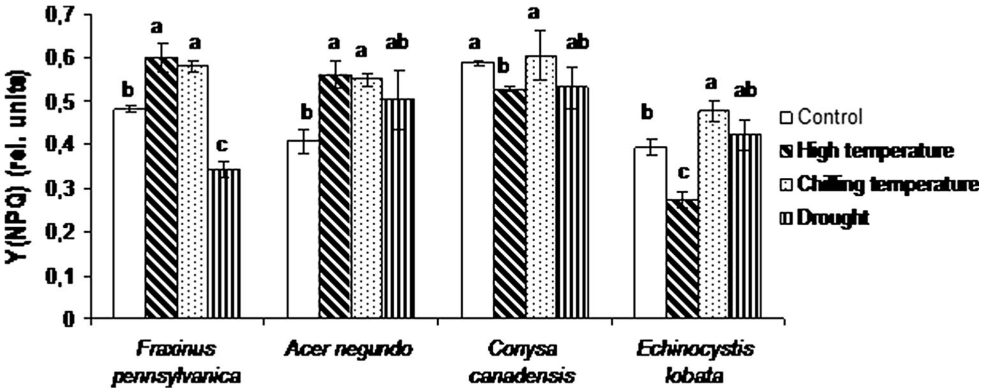

Fig. 6 The quantum yield of non-photochemical light-induced ChlF from woody and herbaceous plants in response to abiotic stresses. *Different letters* within a species indicate significant differences between treatment means (Tukey's test; $P \leq 0.05$)

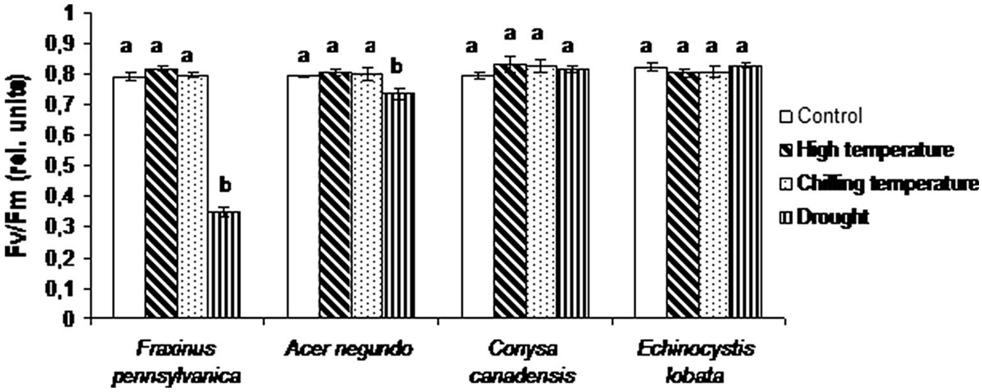

Fig. 7 The maximum quantum yield ChlF from woody and herbaceous plants in response to abiotic stresses. *Different letters* within a species indicate significant differences between treatment means (Tukey's test; $P \leq 0.05$)

predominance of cyclic electron transport. For this reason, the cyclic electron transport rate around PSI could be increased in comparison with the linear electron transport rate (Johnson et al. 2014).

Herbaceous plants showed a slightly different response to stress factors: *C. canadensis* plants showed high tolerance to high, low temperatures, and drought, in which (particularly high temperatures) photochemical processes and oppression of non-photochemical quenching were strengthened. There was an increase in the oxidation of the quinone pool, which helped to activate electron transport between the two photosystems. As a result, this increased Φ_{PSII}. Consequently, there was a decrease in quantum yield NPQ. *E. lobata* was also slightly sensitive to drought because all ChlF indexes did not change relative to the control. However, *E. lobata* plants have similar adaptive photophysiological mechanisms in response to stress as woody plants in response exclusively to chilling.

We have established that the indexes F_v/F_m, q_P, q_N, Φ_{PSII}, Y(NPQ), and Y(NO) can differentiate several aspects of reactions in the photosynthetic apparatus in response to environmental stresses. These indexes may be useful tools for assessing tolerance to plant stress. Most abiotic stresses depressed photochemical quenching of ChlF (except low temperature in *F. pennsylvanica*) while only high and low temperature activated non-photochemical quenching in the leaves of woody plants. The leaves of a herbaceous plant, *C. canadensis*, adopt another mechanism in response to high temperature stress by enhancing PSII activity and suppressing NPQ. We conclude that both woody plants have the same adaptive physiological mechanisms in response to unfavorable temperature while the mechanisms in both herbaceous plants differ, having a higher degree of tolerance to drought than woody plants. The low susceptibility of young invasive plants to abiotic stresses (high, low temperature and drought) may play a key role in determining the invasive ability of these plants.

Author contribution statement ASL and ESS created the experimental idea, conceived and designed the research, and wrote the manuscript. EVT, ESS, and AAL carried out the measurements and performed statistical analyses. JATS wrote the manuscript and participated in design and coordination. All co-authors contributed equally to this work and co-wrote all versions of the manuscript.

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