Pol. J. Environ. Stud. Vol. 31, No. 4 (2022), 3867-3878
DOI: 10.15244/pjoes/146739

Original Research

Comparative Chlorophyll Fluorescence and Growth Responses of two *Amaranthus* Species to Increased N Supply Variability

Tongtong Wang[1], Haixia Han[2], Bin Xie[1], Yuming Feng[1], Yingbo Yu[1], Mei Zhang[1], Fuchen Shi[1]*

[1]College of Life Sciences, Nankai University, Tianjin 30071, China
[2]School of Life Science and Technology, Jining Normal University, Ulanqab 012000, China

Received: 15 December 2021
Accepted: 15 February 2022

Abstract

A pot experiment was conducted to compare the chlorophyll fluorescence (ChlF) and growth performance between invasive *Amaranthus palmeri* S. Watson and its native congener *Amaranthus tricolor* L. under 4 nitrogen (N) supply patterns (control, LN, HN and PN) in monoculture or co-culture. The patterns followed a gradient of increased temporal variability of N supply. The Fv/Fo, QYmax, and Fv'/Fm' of *A. palmeri* were notably higher than *A. tricolor* in monoculture. However, in co-culture, invaders enjoyed these advantages under the CK and LN treatments. The above ChlF parameters of invaders in co-culture significantly decreased except it under the PN treatment. The invader in co-culture possessed the minimal NPQ and maximal 1-qP under the HN and LN treatment respectively. *A. palmeri* also had greater total biomass mainly attributed to its pronounced taller plant height, which contributed super competition abilities to it over congeners. Although the N input improved *A. palmeri*'s growth in co-culture, its ChlF declined under relatively low N variability patterns (LN and HN treatments). Only the higher N variability (PN treatment) promoted invaders' ChlF and growth simultaneously. Results indicated the invasion of *A. palmeri* would be promoted with the increased N supply variability.

Keywords: invasive plant, N supply variability, ChlF parameters, *Amaranthus palmeri*, competitive ability

Introduction

Alien plant invasion attracts increasing attention from ecologists [1-2], as it is posing profound negative impacts and challenges on ecosystem balance and human society's healthy development [3-4]. This event is mainly caused by the introduction of exotic species to a new habitat. However, how to exactly predict and control plant invasions always perplexes most researchers [5]. Normally, invasive plants are highly possible to meet their congeners in a novel environment since they have similar ecological niche demands

---

*e-mail: fcshi@nankai.edu.cn

and inherent biological properties [6]. Therefore, the growth and physiological performance comparison between invasive species and indigenous or non-native congeners (with weak invasiveness) in the same conditions will facilitate the exploration of underlying invasion mechanisms [7-8].

Nitrogen (N) is a macro-element essential for plant growth and development, the plant invasion is highly affected by environmental N conditions [9-10]. Generally, invasive plants tend to use the nutrient more efficiently than native plants when exposed to resources pulse [11]. Correspondingly, Davis [12] proposed the fluctuating resource availability hypothesis holding that high temporal variability in resource (e.g. N) can promote exotic plant invasions. Temporal variability of N supply exists universally across habitats. For example, plant uptakes for N critically rely on the soil moisture, and thus changes in precipitation inevitably increase the temporal variability of N availability [13]. Another example is that different land-use types possess various N input patterns, yielding increased variability as well [14]. Consequently, the rising climate changes and anthropogenic disturbances will predictably generate an increase in the temporal variability of N supply [15-16].

Plant internal N levels could influence the chlorophyll content, which is closely linked to the photosynthetic capacity [17]. It's universally believed that the chlorophyll fluorescence (ChlF) technique is a fast, non-invasive and precise probe for plant photosynthesis function [18-19]. The ChlF is sensitive to different biotic and abiotic stress and plant growth stage, thus it's been widely used in studies of plant photosynthetic apparatus response to environmental changes [20-22]. For example, Wu et al. [23] found that proper timing for N application for star cluster (*Pentas lanceolata*) can be achieved by analyzing ChlF combined with other techniques. Studies of breeding cultivars with resistance to pathogens will be shown by ChlF images [24]. Some experts also use fast ChlF O-J-I-P to demonstrate the heat tolerance in the invasive plant (*Ageratina adenophora*) populations and its high spread potential to tropical areas [25]. Hence, it's practicable to apply the ChlF technique for estimating the photosynthesis performance of invasive plants under various N supply patterns.

Native to the Sonoran Desert in America, *Amaranthus palmeri* S. Watson is an annual C_4 weed in the Amaranthaceae family [26]. *A. palmeri* is a troublesome weed because it can cause significant yield losses in several crops and vegetables because of the dominant competitiveness for resources [27-28]. Meanwhile, chemical control methods for this weed are becoming invalid nowadays as it has evolved resistance to various herbicides [29]. Currently, its spread range has expanded beyond America [30]. In China, *A. palmeri* was first found in Fanzhuangzi Village, Fengtai District, Beijing, in 1985 and was listed as the fourth group of invasive species by the State Environmental Protection Administration of China in 2016 [31]. *A. palmeri* mainly invades the areas in the North China Plain, which covers the main crops cultivation areas and is undergoing expansion to the south and southwest [32]. This weed thrives in the riverbanks, roadsides, open fields, and farmlands, where the N input is temporal heterogeneous [33-34]. *Amaranthus tricolor* L. is a domestic plant widely distributed in China, it can co-occur with *A. palmeri* in the same habitats [35-36]. The present study aimed to (1) analyze the difference in light transport, utilization, and dissipation between two *Amaranthus* species to the increased N supply variability; (2) determine the impact of N temporal variability on their growth performance and competitive ability; and (3) evaluate the invasion of *A. palmeri* in divergent N supply environments by combining the ChlF, growth and competition indexes.

Experimental

Materials and Methods

Experiment Design

Seeds of *A. palmeri* were collected from wild populations along the roadsides in Xiqing District, Tianjin, China (39°02'16"N, 117°4'21"E). Tianjin has a typical temperate and monsoonal climate characterized by hot and rainy summers, cold and dry winters. The annual mean temperature is about 24ºC, the hottest month is July, and the monthly average temperature from June to August is 28ºC. The average annual precipitation is 360-970 mm. Inflorescences bearing massive mature seeds in the healthy invasive plants among several populations were clipped and put in paper bags. The bags were transported to the lab immediately. Inflorescences were air-dried and hand-thrashed in the lab. Plump seeds were obtained according to Schutte's method [37]. Seeds of native *A. tricolor* were purchased from Hebei Qingfeng Seed Co., LTD. The both two *Amaranthus* species seeds were separately stored in glass bottles and kept in dark at 4ºC until use.

Seeds were germinated in the 9-cm Petri dish with moist filter paper placed in. The petri dish was put in an incubator with day and night (d/n) temperature was 30/25ºC and 14 h light. Germinated seeds were then transplanted into a seedling-raising plate, the plate has 72 holes, each hole was filled with 60 g of a mixture of soil and sand at a 3:1 ratio (v/v). The soil was collected from the farmland in Xiqing District (116°57'34"N, 39°08'53"E). The propriety of the mixture contained 1.5% organic matter, 0.05% total nitrogen (TN), 1.29% total carbon (TC). The uniformly sized and vigorous seedlings of each *Amaranthus* species with 4-true-leaf were transplanted to a pot (25×20×20 cm). Every pot had 3.8 kg the same mixture as the plate with a pH value of about 7.9. The experiment had two modes of competition treatment (monoculture and co-culture):

for monoculture, each pot contained four *A. palmeri* or *A. tricolor* seedlings, whereas for co-culture, two seedlings of *A. palmeri* and two seedlings of *A. tricolor* grown together in the same pot.

After the preculture of two weeks, 100 mL NH_4NO_3 (GR,>99%; Fuchen Chemical Reagent Co., Ltd, Tianjin, China) solution was applied six times to create four different temporal N supply patterns: no N supply treatment (CK), constant low N supply treatment (LN), constant high N supply treatment (HN), pulsed N supply treatment (PN). The N supply variability increased from the control to the PN treatment. The LN treatment was totally supplied with 0.18g N per pot, and the HN and PN treatments received the same total N amounts as 0.36g per pot. The amount and time of N supply at each time were shown in Table 1. The experiment was performed in a greenhouse at Nankai University (Tianjin, China, 39°06'09"N, 117°10'02"E) from June 22 to August 28, 2020. Thirty-six pots were randomly placed in a greenhouse with a glass rooftop and wire netting walls, so it can let the sunlight and ambient air pass but prevent disturbances from birds and rains. All pots were watered with 100 mL distilled water once a day and moved biweekly over the duration of the experiment.

Chlorophyll Fluorescence and Growth Performance Parameters Measurements

The sixth fully developed leaf from the top was chosen to measure the ChlF parameters by Portable Handy FluorCam (Ecotech Ecological Technology Ltd. USA) at 9:00-12:00 h. We set the protocols of the FluorCam as Shutter = 0, Sensitivity = 20, AChlt2 = 100, AChlt1 = 100, Super = 70 according to results of preliminary experiments and previous research [38]. Before the measurement, the leaves were adapted to darkness for 25 min.

The initial fluorescence (Fo) under dark adaptation was measured with a weak measuring radiation. The maximal fluorescence (Fm) under dark adaptation was measured by giving saturated pulse radiation. Saturation pulse radiation was turned on to measure the maximal fluorescence (Fm') under light adaptation. Turn off photochemical radiation and turn on far-red radiation to measure the minimum fluorescence (Fo') under light adaptation. The variable fluorescence (Fv) in the dark-adapted state was calculated as Fm-Fo, and the variable fluorescence (Fv') under light adaptation was calculated as Fm'-Fo'.

The potential photochemical efficiency (Fv/Fo) was calculated as (Fm-Fo)/Fo, these parameters reflect the potential activity of the PSII [39]. The maximum quantum yield of PSII photochemistry in dark, QYmax = Fv/Fm, reflects the maximum efficiency to transform the light absorbed by PSII [40]. The effective quantum yield of PSII photochemistry in the light, Fv'/Fm' = (Fm'-Fo')/Fm', indicates the primary efficiency at which light absorbed by PSII is used for photochemistry, which is the PSII operating efficiency when all the PSII centers were open (primary quinone electron acceptor-Q_A oxidized) [19]. The electron transport rate (ETR) was calculated as ΦPSII × 0.84 × PAR × 0.5, where 0.84 is the average absorbance of leaves and 0.5 is the PAR (Photosynthetically Active Radiation) is equally absorbed by photosystems I and II [41]. ETR indicates the apparent photosynthetic electron transport rate which is leading to carbon fixation, it's proportional to the photosynthetic activity [42].

Non-photochemical quenching (NPQ) was calculated as follows: NPQ = (Fm-Fm')/Fm', its value varies from 0 to infinity, this parameter means the process that excess light excitation energy in PSII is dissipated non-radiatively by heat [43]. The excitation pressure (1-qP) was obtained as 1-(Fm'-Fs)/(Fm'-Fo'), this index indicated the state of reduction of plastoquinone pool at the PSII receptor side and the balance between energy supply and utilization [44].

Plant height was measured as the distance from the soil surface to the shoot tips. Plants were then harvested and separated as shoots and roots, the total biomass was weighed after oven-dried at 80ºC for 72 h.

The relative biomass (RB) was determined by the following formula [45] to measure the competitive effects between invasive and native *Amaranthus* species under various N supply variability treatments. The RB was calculated as $RB_{ij} = B_{ij}/B_{ii}$, where B_{ij} is the biomass production of species i when it grown in co-culture with species j, B_{ii} is the biomass production of species i when it grown in monoculture. RB>1

Table 1. Different temporal N supply variability patterns.

Treatment	Date and content of nitrogen application per pot each time						Total nitrogen input content
	0 DAT	12th DAT	24th DAT	36th DAT	48th DAT	60th DAT	
CK	0 g	0 g	0 g	0 g	0 g	0 g	0 g
LN	0.03 g	0.03 g	0.03 g	0.03 g	0.03 g	0.03 g	0.18 g
HN	0.06 g	0.06 g	0.06 g	0.06 g	0.06 g	0.06 g	0.36 g
PN	0.03 g	0.09 g	0.03 g	0.09 g	0.03 g	0.09 g	0.36 g

DAT: days after treatment. CK, control; LN, plants growing constant low N supply pattern; HN, plants growing constant high N supply pattern; PN, plants growing pulsed high N supply pattern.

indicates that the species i outperformed species j under the competition situation. RB<1 indicates that species i underperformed species j under the competition situation [46]. A high value of RB indicates the strong competitive capacity of the species [47].

Statistical Analysis

The means of three replicates and their standard deviation (SD) were determined. Differences of two species under various N supply patterns were determined by the pairwise comparison analysis in Generalized Linear Model (GLM) at $P<0.05$. Each ChlF parameter and growth index was set as an independent variable, the N supply treatments and cultivation types together were set as a dependent variable. To analyze the relative biomass differences due to various N supply conditions, an analysis of Duncan at $P<0.05$ was also performed, with the N supply as the independent variable and the relative biomass as the dependent variable. All data were analyzed using SPSS 20.0 for windows (SPSS Inc.). A reference sequence that was a little higher than the optimal measured values of each parameter was achieved. Because the Fo and 1-qP were negative with the performance of plants, the reciprocal of the two parameters was adopted in the analysis process. Then the measured values of each parameter were set as a comparison sequence. After the dimensionless processing, the data were analyzed by the Gray Relation Analysis (GRA) in Excel 2003 (Microsoft Cor).

Results and Discussion

Differences in Fo, Fm, and Fv between *A. palmeri* and *A. tricolor* under Various N Supply Variability Patterns

The exogenous N supply variability increased the Fo, Fm, and Fv of plants in both cultivation types, but a decline in these parameters of the *A. palmeri* in co-culture was observed (Table 2). If the N was supplied at a constant low rate (LN treatment), the three ChlF parameters of the two *Amaranthus* species in monoculture all reached the peak values. However, in co-culture, the ChlF parameters of *A. palmeri* were at the highest when plants were grown under control; the Fo and Fm values of *A. tricolor* were at the highest when N supply was at a constant high rate (HN treatment), and the Fv reached the maximal value under the pulsed N supply condition (PN treatment). The Fo, Fm and Fv of plants grown in monoculture were all higher than it in co-culture respectively, except the Fv of natives under the greatest N supply variability (PN treatment). The three ChlF parameters of *A. palmeri* were both significantly higher in the monoculture than in co-culture when supplied with exogenous N. All the ChlF parameters of invaders were significantly higher than natives in co-culture under all N supply patterns with the exception of Fm under the constant low N supply treatment (Table 2).

Table 2. Variation of the Fo, Fm, and Fv of *A. tricolor* and *A. palmeri* growing under different N supply patterns and cultivation types.

		CK	LN	HN	PN
Fo	NM	185.25±34.69 c	283.92±36.26 a	225.91±35.60 b	233.72±39.00 b
	IM	146.42±21.22 d	178.34±32.72 cd	145.23±13.89 d	161.04±25.55 cd
	NC	119.29±15.38 de	138.96±23.84 d	216.99±29.97 bc	140.00 ±24.27 d
	IC	126.34±16.49 de	97.70±8.94 e	122.47±18.74 de	88.13±14.05 e
Fm	NM	273.30±40.24 c	442.95±52.90 a	352.16±57.51 b	358.91±58.74 b
	IM	257.88±37.75 e	331.94±43.79 b	257.07±24.89 e	310.21±53.15 b
	NC	205.93±25.24 f	181.44±18.73 f	328.79±36.77 b	271.14±37.60 de
	IC	232.84±27.86 ef	162.18±19.20 f	189.63±28.23 f	173.41±25.91 f
Fv	NM	88.05±5.58 cd	159.03±23.11 a	126.25±22.62 b	125.19±20.22 b
	IM	111.46±17.04 b	153.60±13.46 a	111.84±11.00 b	149.17±28.24 ab
	NC	86.64±11.86 cd	42.48±5.55 f	111.80±8.50 b	131.14±15.66 b
	IC	106.50±11.82 c	64.49±10.27 e	67.15±11.57 d	85.27±14.14 d

Data were shown mean±SD, *n* = 3. Dissimilar lowercase letters indicate significant differences between various N supply treatments for the two *Amaranthus* species under divergent cultivation types ($P<0.05$). Fo, initial fluorescence; Fm, maximal fluorescence; Fv, variable fluorescence. NM, native *A. tricolor* was grown in monoculture; IM, invasive *A. palmeri* was grown in monoculture; NM, native *A. tricolor* was grown in co-culture; IM, invasive *A. palmeri* was grown in co-culture. CK, control; LN, plants growing constant low N supply pattern; HN, plants growing constant high N supply pattern; PN, plants growing pulsed high N supply pattern.

Different Light Energy Utilization Responses of two *Amaranthus* Species to Various N Supply Temporal Variability

The N supply slightly decreased the Fv/Fo, ETR, QYmax and Fv'/Fm' of the *A. tricolor* in monoculture, except the Fv/Fo and QYmax under the constant high N supply treatment (Fig. 1). The Fv/Fo and QYmax of *A. palmeri* in monoculture under the LN and PN treatments were all higher than that under the control and HN conditions, and the increase in Fv/Fo was significant ($P<0.05$). The N input decreased the Fv'/Fm' but significantly promoted the ETR of *A. palmeri* in monoculture ($P<0.05$; Fig. 1b, d). The ChlF parameters of *A. tricolor* under the LN treatments were all lower than control in co-culture, moreover the reduction in Fv/Fo and Fv'/Fm' was remarkable ($P<0.05$). By contrast, the greatest N supply variability sharply improved the ChlF of *A. tricolor* in co-culture ($P<0.05$; Fig. 1). The four ChlF parameters of *A. palmeri* in co-culture were significantly lower under the constant low and high N supply treatments than under the control and pulsed N supply treatments, the greatest N supply variability improved these indexes, and the increases in Fv/Fo and ETR were notable ($P<0.05$; Fig. 1). The four ChlF parameters of two species in co-culture and *A. palmeri* in monoculture were highest under the greatest N supply variability.

In monoculture, the ChlF parameters of *A. palmeri* were significantly higher than *A. tricolor* under all treatments except the ETR and QYmax under the HN treatment, while a dramatic opposite relationship about ETR was detected under control ($P<0.05$; Fig. 1). In co-culture, the Fv/Fo, ETR, QYmax, and Fv'/Fm' of *A. palmeri* were all significantly greater than *A. tricolor* under the control and LN treatments. Besides the differences of ETR under the PN treatment and Fv'/Fm' under the HN treatment were also pronounced ($P<0.05$; Fig. 1).

The Fv/Fo, ETR, QYmax, and Fv'/Fm' of *A. tricolor* were all greater in monoculture than in co-culture under the control, LN, and HN patterns, except the Fv/Fo under the control treatment and QYmax under the HN treatment (Fig 1). Furthermore, some of the improvements were significant, but a contrast comparison relationship of those ChlF parameters existed under the pulsed N supply treatment ($P<0.05$; Fig. 1). The ChlF indexes of *A. palmeri* in monoculture under the control and PN treatments were all lower than that in co-culture. However, if the N was supplied at a constant rate (LN and HN treatments), the relationships between the two cultivation types were sharply contrary. Meanwhile, the differences in ETR of *A. palmeri* between two cultivars under all the N supply patterns were significant ($P<0.05$; Fig. 1b).

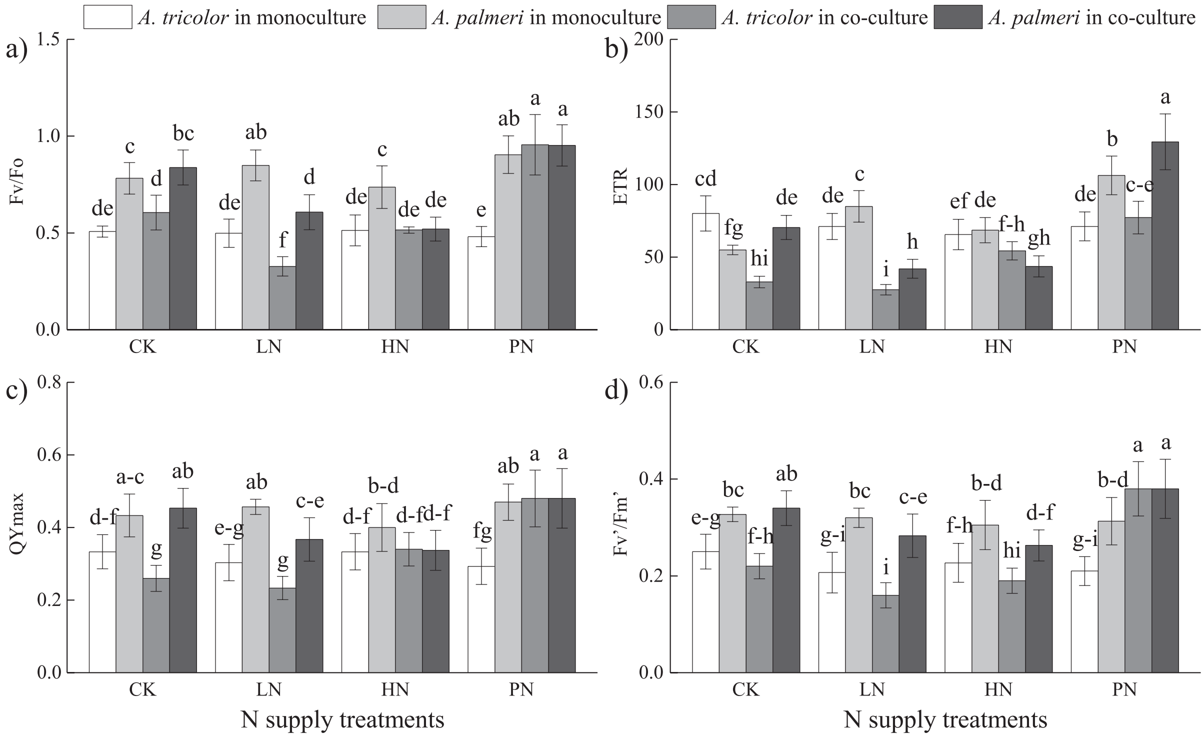

Fig. 1. The Fv/Fo, ETR, QYmax, and Fv'/Fm' of *A. tricolor* and *A. palmeri* growing in the two cultivation types under increased temporal N supply variability treatments. All bars in the figure show mean±SD, $n = 3$. Dissimilar lowercase letters indicate significant differences between various N supply treatments for the two *Amaranthus* species under divergent cultivation types ($P<0.05$). Fv/Fo, potential photochemical efficiency; ETR, electron transport rate; QYmax, the maximum quantum yield of PSII; Fv'/Fm', effective quantum yield of PSII. CK, control; LN, plants growing in constant low N supply pattern; HN, plants growing in constant high N supply pattern; PN, plants growing in pulsed high N supply pattern.

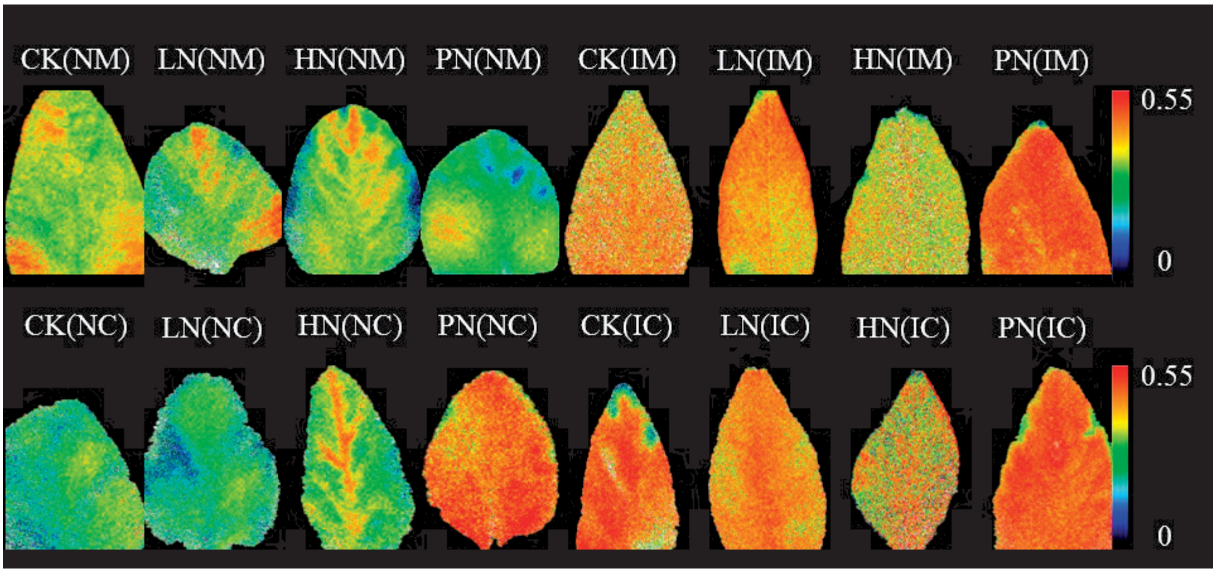

Fig. 2. The QYmax images of the two *Amaranthus* species leaves under different N supply treatments and cultivation types. QYmax, the maximum quantum yield of PSII. CK, control; LN, plants growing in constant low N supply pattern; HN, plants growing in constant high N supply pattern; PN, plants growing in pulsed high N supply pattern. NM: native *A. tricolor* growing in monoculture; IM: invasive *A. palmeri* growing in monoculture; NC: native *A. tricolor* growing in co-culture; IC: invasive *A. palmeri* growing in co-culture. The value of the color bar ranges from 0 to 0.55 with the color ranges from blue to orange.

The maximum value of the color bar was 0.55 and the minimum value was 0, the corresponding color was orange and blue respectively, and the green represented a median value (Fig. 2). If the leaf had larger orange areas, it tended to have a higher QYmax which indicated the light energy conversion efficiency of PSII was greater. While the blue region revealed the reaction center of PSII in this part was damaged or even inactivated. The comparison results of different color sizes in the QYmax images were entirely consistent with the pattern demonstrated by Fig. 2.

Different Non-Photochemical Quenching and Light Reactions Damage in PSII of Two *Amaranthus* Species under Various N Temporal Supply Patterns

The NPQ of *A. tricolor* significantly improved by the N supply treatment, except it in monoculture under pulsed N supply treatment (Fig 3a). The N input also significantly promoted the NPQ of *A. palmeri* grown alone, but the NPQ value under HN treatment decreased (Fig 3a). The NPQ of *A. palmeri* in co-culture was significantly inhibited under the relative low N supply variability (LN and HN treatments), but the greatest variability increased the NPQ values. Exogenous N supply decreased the 1-qP of *A. tricolor* in co-culture and *A. palmeri* in monoculture but increased the values of the two species in monoculture and co-culture respectively except the *A. palmeri* under the greatest variability. It's noted that the greatest N supply variability significantly declined the 1-qP of *A. palmeri* in two cultivation modes and *A. tricolor* in co-culture ($P<0.05$; Fig 3b).

The NPQ of plants in monoculture was both higher than that in co-culture under all the N treatments, but the comparison relationship was converse for *A. palmeri* under control and *A. tricolor* in the HN treatment ($P<0.05$). The 1-qP was higher in co-culture than in monoculture for both *Amaranthus* species except the *A. palmeri* under control. Differences in NPQ and 1-qP between two cultivation types under the constant low N supply treatment were both significant ($P<0.05$; Fig. 3).

For plants in monoculture, the NPQ and 1-qP of *A. palmeri* were higher than *A. tricolor* under all conditions except the NPQ under the HN treatments and 1-qP under the PN treatments (Fig 3). Moreover, the advantages of *A. palmeri* over *A. tricolor* in NPQ under the control, LN, and HN treatments were notable ($P<0.05$). In co-culture, the NPQ of *A. palmeri* was greater under control but lower under the LN, HN, and PN treatments than *A. tricolor*. However, the relationship of 1-qP between two *Amaranthus* species under the control, LN, and HN treatments was contrary to the NPQ ($P<0.05$; Fig 3).

Distinct Growth Performance of Native *Amaranthus* Species and Invasive *Amaranthus* Species under Divergent N Variability

The plant height of the plants in both cultivation types increased under the exogenous N input treatments except *A. palmeri* under the LN treatment and *A. tricolor* under the PN treatment in co-culture. Remarkably, the increase of *A. palmeri* was sharp ($P<0.05$; Fig. 4a). The two *Amaranthus* species accumulated more

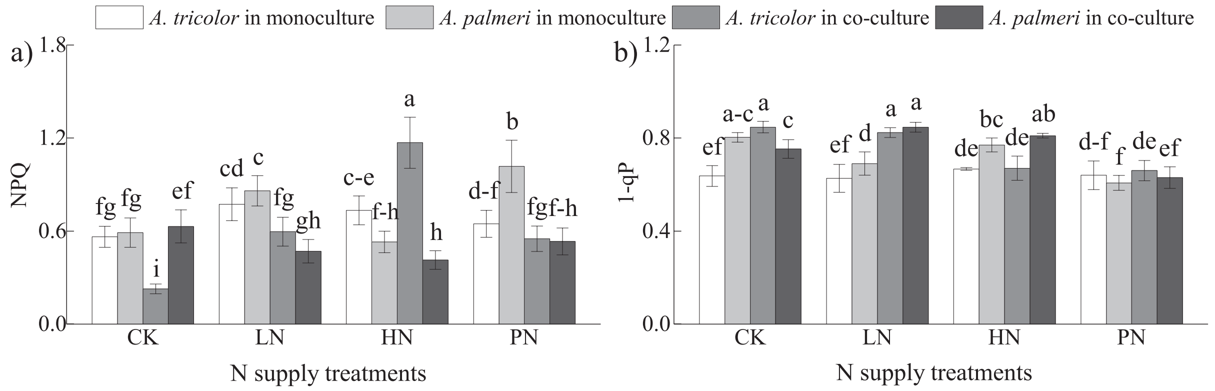

Fig. 3. The NPQ and 1-qP of *A. tricolor* and *A. palmeri* growing in the two cultivation types under increased temporal N supply variability treatments. All bars in the figure show mean±SD, n = 3. Dissimilar lowercase letters indicate significant differences between various N supply treatments for the two *Amaranthus* species under divergent cultivation types ($P<0.05$). NPQ, non-photochemical quenching; 1-qP, excitation pressure. CK, control; LN, plants growing in constant low N supply pattern; HN, plants growing in constant high N supply pattern; PN, plants growing in pulsed high N supply pattern.

biomass under various N supply patterns compared with control. And the improvements in total biomass of *A. tricolor* in monoculture and *A. palmeri* in co-culture were pronounced ($P<0.05$; Fig. 4b). The plants in co-culture reached maximal biomass under the pulsed N supply condition, while *A. tricolor* and *A. palmeri* in monoculture reached the optimal values under the constant high or low N supply treatments respectively.

The height of *A. tricolor* was higher in monoculture than in co-culture under all conditions and the divergences under the control, LN, and PN treatments were significant ($P<0.05$; Fig. 4a). For *A. palmeri*, the plant in monoculture was significantly shorter than that in co-culture with an opposite mode of it under the LN treatment ($P<0.05$). The biomass of *A. palmeri* in co-culture was significantly greater than it in monoculture, but that of *A. tricolor* in co-culture was significantly lower than it in monoculture ($P<0.05$; Fig. 4b). The height and total biomass were sharply greater of *A. palmeri* than of *A. tricolor* in the same cultivation types ($P<0.05$; Fig. 4).

Divergent Competition Response between Native *Amaranthus* Species and Invasive *Amaranthus* Species to Various N Supply Variability Conditions

The RB of *A. palmeri* was all greater than 1 and significantly higher than that of *A. tricolor*, the value even beyond 2 under the PN treatment ($P<0.05$; Fig. 5). There was no significant difference in RB of *A. tricolor* under the all N supply treatments compared with the control, but RB of individuals under the pulsed N supply treatment was much greater than that under the constant N supply treatments ($P<0.05$). And RB of *A. palmeri* under the greatest N supply variability was the highest among all the N supply patterns ($P<0.05$; Fig. 5).

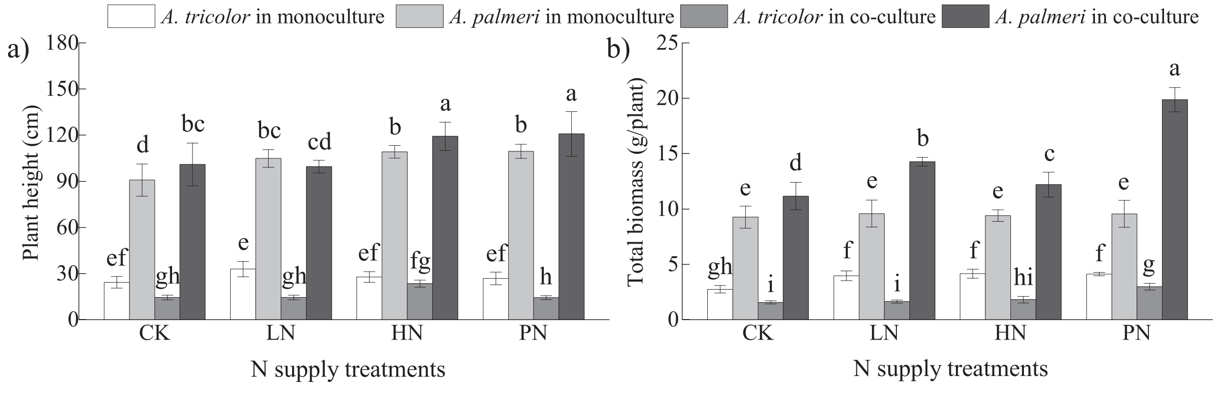

Fig. 4. The plant height (cm) and total biomass (g/plant) of *A. tricolor* and *A. palmeri* growing in the two cultivation types under increased temporal N supply variability treatments. All bars in the figure show mean±SD, n = 3. Dissimilar lowercase letters indicate significant differences between various N supply treatments for the two *Amaranthus* species under divergent cultivation types ($P<0.05$). CK, control; LN, plants growing in constant low N supply pattern; HN, plants growing in constant high N supply pattern; PN, plants growing in pulsed high N supply pattern.

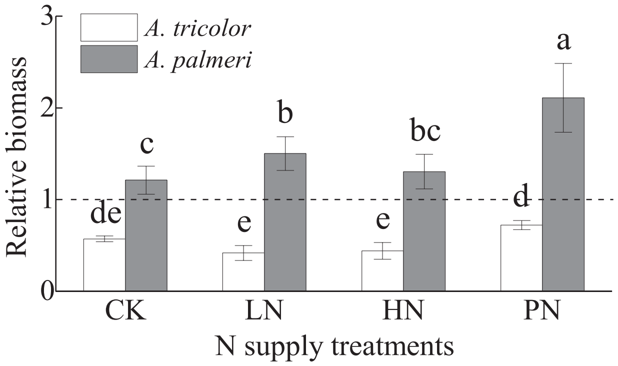

Fig. 5. Effects of different N supply treatments and cultivation types on the relative biomass of the individual plant *A. tricolor* and *A. palmeri* . All bars in the figure show mean±SE, *n* = 3. Dissimilar lowercase letters indicate significant differences between various N supply treatments for the two *Amaranthus* species under divergent cultivation types ($P<0.05$). CK, control; LN, plants growing in constant low N supply pattern; HN, plants growing in constant high N supply pattern; PN, plants growing in pulsed high N supply pattern.

Correlation of Fluorescence Parameters and Growth Performance of Two *Amaranthus* Species under Diverse N Supply

The GRA results showed that responses in the ChlF and growth indices of *A. palmeri* were much more positive to the N input treatments than *A. tricolor* in both two cultivation types, except *A. palmeri* in co-culture under the HN treatment which was at the low order (Table 3). The GRA results showed that gray correlative degree (GCD) and equal weight order (EWO) in the ChlF and growth of *A. palmeri* was much greater than *A. tricolor* under all N supply treatments in both two cultivation modes, an exception from this pattern was detected in *A. palmeri* only in co-culture under the HN treatment (Table 3). And the invasive species in monoculture had greater GCD and EWO than it in co-culture under the LN and HN treatments, however, native plants in co-culture had greater GCD and EWO under the HN and PN treatments than in monoculture. The GRA results also revealed that plants all maximized their GCD and EWO under the greatest N supply variability, but the *A. tricolor* in monoculture reached the peak values under the constant low N supply treatment (Table 3).

Discussions

The chlorophyll fluorescence technique is an ideal probe reflecting the state of PSII, Fo, Fm, and Fv which are three basic parameters of ChlF [19]. The Fo represents the minimal or primary fluorescence when all functional centers of PSII are open, it would increase when plants are in a stressful environment [39]. The up-regulation of Fo in this study indicated the situation of *A. palmeri* in monoculture and *A. tricolor* in two cultivation types became unfavorable with exogenous N supply. This is probably because the interspecific and intraspecific competition turned out to be more aggressive as the growth and photosynthesis of plants were dramatically promoted by N input [48]. However, considering *A. tricolor* was a weak competitor causing little interspecific pressure to *A. palmeri*, the Fo of *A. palmeri* in co-culture under the N input conditions was lower compared with it under the control and other plants in this experiment (Table 2).

The Fv/Fo, QYmax and Fv'/Fm' mean the potential activity, maximum quantum yield, and effective quantum yield of PSII respectively [38]. And the ETR indicates the activity of PSII and carbon fixation of plants [42, 49]. The variation in these ChlF parameters could reflect the change in the absorption,

Table 3. Grey correlative degrees of ChlF parameters, plant height and total biomass between two *Amaranthus* species and reference series.

	N supply patterns			
	CK	LN	HN	PN
GCD of *A. tricolor* in monoculture	0.4711	0.5309	0.4956	0.4870
EWO of *A. tricolor* in monoculture	14	7	11	13
GCD of *A. palmeri* in monoculture	0.5376	0.5802	0.5256	0.5953
EWO of *A. palmeri* in monoculture	6	3	8	2
GCD of *A. tricolor* in co-culture	0.4665	0.4366	0.4986	0.5679
EWO of *A. tricolor* in co-culture	15	16	10	4
GCD of *A. palmeri* in co-culture	0.5531	0.5172	0.4884	0.6518
EWO of *A. palmeri* in co-culture	5	9	12	1

Gray correlative degree (GCD), equal weight order (EWO). CK, control; LN, plants growing in constant low N supply pattern; HN, plants growing in constant high N supply pattern; PN, plants growing in pulsed high N supply pattern.

transformation, and transport of the PSII for the light energy. A notable superiority in the Fv/Fo, QYmax, ETR, and Fv'/Fm' of *A. palmeri* beyond *A. tricolor* was detected under all the N supply variability patterns in monoculture, showing invaders had remarkable higher fluorescence characteristics and photosynthetic capacity that mainly result from the difference in plant species. Although the two *Amaranthus* species were C_4 plants with a higher N use efficiency [50], *A. palmeri* had an apparent greater sunlight utilization and electron transfer efficiency than natives especially under control, LN, and PN concentrations when in monoculture (Fig 1). This was the same as the research of Guo [51] about *A. palmeri* had a higher Fv/Fm (QYmax) than *Amaranthus retroflexus* and *Amaranthus rudis* at 35/30ºC treatments. Whereas the pronounced advantage in the ChlF of *A. palmeri* over *A. tricolor* disappeared when they were grown together under high N supply patterns, and the index of *A. palmeri* decreased with the N input concentration increased (Fig 1). The possible reason was that *A. tricolor* was poor at resource competition, thus the constant high N supply treatments perhaps exceeded the maximal absorption of the *A. palmeri'* causing the high N stress and reducing the ChlF of *A. palmeri* [52]. Most notably, both two species caught a much higher and similar ChlF under the PN treatment, this was consistent with the previous studies [53]. Perhaps because the greatest temporal variability of N supply fitted in with the N consumption demand of two *Amaranthus* species at different development stages, thus ChlF of the two species was promoted mostly under this pattern. And ChlF differences between them were narrowed as the promotion in ChlF of natives was unexpectedly higher than it of invaders.

The NPQ states one part of excess absorbed light energy which can not be transported by electrons but can be dissipated in the form of heat [43]. It's one of the most important protection mechanisms helping plants to avoid photodamage caused by biotic and abiotic stresses [54]. The NPQ of *A. palmeri* in monoculture and *A. tricolor* increased under the increased N supply variability, but that of *A. palmeri* in co-culture decreased with N supply variability and was the lowest in each treatment group. Usually, the relations between NPQ and Fv'/Fm' of healthy leaves were negative, if a decreasing Fv'/Fm' met a declining NPQ then the structure and function of PSII were probably broken [39]. The NPQ variation demonstrated that invaders grown alone and natives had great NPQ efficiency to protect it from the damage to PSII under the increased N supply variability. However, invaders' abilities to dissipate excessive excitation energy were sharply inhibited by N supply in co-culture, this may be related to the plant growth cycle [52]. The 1-qP (excitation pressure) is an estimate of the redox state of the electron acceptor (Q_A) of PSII and thus reflects the balance between energy supply and utilization in PSII [55]. Vlčková et al. [56] found that the senescent plant up-regulated the 1-qP and excitation pressure could be an indicator of senescence. The 1-qP of invaders was greater than natives especially under the HN condition, but this relationship was converse under the PN treatment. Notably, the N supply in pulses dramatically decreased the 1-qP of natives in co-culture and invaders in both cultivation modes. Similarly, previous studies found excitation pressure mediated plant natural senescence and premature senescence caused by detrimental N status [57]. Thus, it's believed that senescence led to the decrease in NPQ and the increase in 1-qP of *A. palmeri* under constant N supply conditions in co-culture, but the greatest N supply variability treatment delayed senescence and improved the ChlF indexes of two *Amaranthus* species.

The higher photosynthetic and CO_2 assimilation capacity of plants were motivated by elevated N supply, as it can increase the stromal and thylakoid proteins contents in chloroplasts [58]. Further, invasive plants attributed more resources to photosynthesis and hence utilized resources more efficiently and grow faster [9]. Stronger and healthy photosynthesis is essential to the growth improvement of green plants. Previous studies have demonstrated that invasive *Amaranthus* species always had greater nutrient competitive abilities, sunlight in particular, through the super plant height [59]. Thus, prominent advantages in plant height of *A. palmeri* than *A. tricolor* also can be found in this study regardless of cultivation types (Fig 4a). But invaders grew taller in co-culture than in monoculture which conflicts with the ChlF performance in the LN and HN treatments (Figs 1, 4). Khangura et al. [60] demonstrated a nonlinear relationship between the plant height and chlorophyll levels, so a low ChlF performance would not lead to a shorter *A. palmeri* height under the relative lower N supply variability. Previous studies also found that *A. palmeri* could produce much more leaves placed vertically to the ray of the sun than *A. tricolor*, improving invaders' whole photosynthetic efficiency that's able to grow longer stems [36, 61]. Therefore, the ChlF reduction at single leaf levels might have little influence on invaders' growth under the lower N supply variability patterns, but the ChlF and dry matter accumulations of invaders improved notably under the pulsed N input treatment. The same results could be found in former studies [45]. The taller height and greater biomass contributed the superior relative biomass (RB) to *A. palmeri* than *A. tricolor* under all treatments, and RB values proposed the powerful competition abilities of invaders and were in line with former studies [35]. It should be pointed out that the higher RB of plants under the greatest N supply variability in co-culture may attribute to the significant improvement in ChlF performance yielding much biomass accumulation.

Following the analysis principle of correlative degree in gray system theory, the reference group is an ideal model responding to the increased N supply temporal variability most positively [62]. So, a higher GCD between the reference group and a treatment group represents this group was more actively sensitive to the N supply variability compared with the other groups. In this study, invaders reacted more vigorously to the exogenous N supply treatment. The results were in agreement with the findings of Wang et al [63]. Besides, *A. palmeri* under the HN treatment in co-culture had low EWO, this was mainly due to the sharp decrease in ChlF parameters and features of equal weight order [64].

Conclusions

The objective of this study was to gain insights into the differences in ChlF and growth responses of invasive *A. palmeri* and native *A. tricolor* to the increased temporal N supply variability and evaluate the invasion of *A. palmeri* under such conditions. The result showed that *A. palmeri* possessed the notably higher Fv/Fo, ETR, QYmax, and Fv'/Fm', conferring the greater light energy transport and utilization efficiency to invaders in monoculture and under low N supply variability in co-culture. Moreover, the greatest N supply variability (PN treatment) sharply improved the photosynthetic efficiency of the two *Amaranthus* species in co-culture and thus diminished the difference between them. The higher NPQ of invaders could facilitate a more efficient excess light energy dissipation in monoculture, but this photoprotection mechanism was more effectively operated by natives in co-culture. The N supply variability contributed to dramatically greater plant height and total biomass of *A. palmeri*, which can help invader to establish competitive dominance and boost its growth performance in turn. The GRA results suggested that ChlF and growth responses of *A. palmeri* were more active than *A. tricolor* and more positive to the PN treatment, thus the invasion of *A. palmeri* will be aggravated under N supply conditions especially with greater temporal variability.

Acknowledgments

This work was supported by the project of the Tianjin Agricultural Committee, China (No. ITTFPRS2018001).

Conflict of Interest

The authors declare no conflict of interest.

References

1. SUDA J., MEYERSON L.A., LEITCH I.J., PYŠEK P. The hidden side of plant invasions: the role of genome size. New Phytol., **205** (3), 994, **2015**.
2. ZHANG W.X., YIN D., HUANG D.Z., DU N., LIU J., GUO W.H., WANG R.Q. Altitudinal patterns illustrate the invasion mechanisms of alien plants in temperate mountain forests of northern China. For. Ecol. Manage., **351**, 1, **2015**.
3. CANAVAN K., CANAVAN S., HARMS N.E., LAMBERTINI C., PATERSON I.D., THUM R. The potential for biological control on cryptic plant invasions. Biol Control, **144**,104243, **2020**.
4. BÉLOUARD N., PAILLISSON J.M., OGER A., BESNARD A.L., PETIT E.J. Genetic drift during the spread phase of a biological invasion. Mol. Ecol., **28**, 4387, **2019**.
5. DUNCAN J.P., ROZUM R.N., POWELL J.A., KETTENRING K.M. Multi-scale methods predict invasion speeds in variable landscapes. Theor. Ecol., **10** (3), 287, **2017**.
6. LU X.M., SIEMANN E., HE M.Y., WEI H., SHAO X., DING J.Q. Warming benefits a native species competing with an invasive congener in the presence of a biocontrol beetle. New Phytol., **211** (4), 1371, **2016**.
7. WANG K., YANG J., CHEN J. The applications of congeneric comparisons in plant invasion ecology. Biodiv. Sci., **17** (4), 353, **2009**.
8. HAMANN E., KESSELRING H., STÖCKLIN J. Plant responses to simulated warming and drought: a comparative study of functional plasticity between congeneric mid and high elevation species. J. Plant Ecol, **11** (3), 364, **2018**.
9. LUO Y.J., GUO W.H., YUAN Y.F., LIU J., DU N., WANG R.Q. Increased nitrogen deposition alleviated the competitive effects of the introduced invasive plant Robinia pseudoacacia on the native tree *Quercus acutissima*. Plant Soil, **385** (1-2), 63, **2014**.
10. HE F., XIE K., LI X . Effect of Nitrogen Fertilizer and Seeding Rate on Yield of Alfalfa and Weeds. Pol. J. Environ. Stud., **27** (2), 647, **2017**.
11. PAREPA M., KAHMEN A., WERNER R.A., FISCHER M., BOSSDORF O. Invasive knotweed has greater nitrogen-use efficiency than native plants: evidence from a ^{15}N pulse-chasing experiment. Oecologia, **191** (2), 389, **2019**.
12. DAVIS M.A., GRIME J.P., THOMPSON K. Fluctuating resources in plant communities: a general theory of invasibility. J. Ecol., **88** (3), 528, **2000**.
13. DONG C., WANG W., LIU H., XU X., CHEN X., ZENG H. Comparison of soil microbial responses to nitrogen addition between ex-arable grassland and natural grassland. J. Soils Sediments, **21** (3), 1371, **2021**.
14. DONG B.Q., QIN T.L., WANG Y., ZHAO Y., LIU S.S., FENG J.M., LI C.H., ZHANG X. Spatiotemporal variation of nitrogen and phosphorus and its main influencing factors in Huangshui River basin. Environ. Monit. Assess., **193** (5), 292, **2021**.
15. PAREPA M., FISCHER M., BOSSDORF O. Environmental variability promotes plant invasion. Nat. Commun., **4**, 1604, **2013**.
16. ALTMAN I., BYERS J.E. Large-scale spatial variation in parasite communities influenced by anthropogenic factors. Ecology, **95** (7), 1876, **2014**.
17. TANTRAY A.Y., BASHIR S.S., AHMAD A. Low nitrogen stress regulates chlorophyll fluorescence in coordination with photosynthesis and Rubisco efficiency of rice. Physiol. Mol. Biol. Plants, **26** (3), 83, **2019**.
18. ZHANG S.R. A discussion on chlorophyll fluorescence kinetics parameters and their significance. Chin. Bull. Bot., **16** (4), 444, **1999**.
19. BAKER N.R. Chlorophyll fluorescence: a probe of photosynthesis in vivo. Annu. Rev. Plant Biol., **59** (1), 113, **2008**.

20. LIN Y.C., H Y.G., Ren C.Z., GUO L.C., WANG C.L., JIANG Y., WANG X.J., PHENDUKANI H., ZENG Z.H. Effects of nitrogen application on chlorophyll fluorescence parameters and leaf gas exchange in naked oat. J. Integr. Agric., **12** (12), 2164, **2013**.
21. CENDRERO-MATEO M.P., CARMO-SILVA A.E., PORCAR-CASTELL A., AMERLYNCK E.P., PAPUGA S.A., MORAN M.S. Dynamic response of plant chlorophyll fluorescence to light, water and nutrient availability. Funct. Plant Biol., **42**, 746, **2014**.
22. DABROWSKI P., BACZEWSKA A.H., PAWLUSKIEWICZ B., PAUNOV M., ALEXANTROV V., GOLTSEV V., KALAJI M.H. Prompt chlorophyll a fluorescence as a rapid tool for diagnostic changes in PSII structure inhibited by salt stress in Perennial ryegrass. J. Photochem. Photobiol. B-Biol., **157**, 22, **2016**.
23. WU C.W., LIN K.H., LEE M.C., PENG Y.L., CHOU T.Y., CHANG Y.S. Using chlorophyll fluorescence and vegetation indices to predict the timing of nitrogen demand in *Pentas lanceolata*. Korean J. Hortic. Sci. Technol., **33** (6), 845, **2015**.
24. BAURIEGEL E., BRABANDT H., GARBER U., HERPPICH W.B. Chlorophyll fluorescence imaging to facilitate breeding of *Bremia lactucae*-resistant lettuce cultivars. Comput. Electron. Agric., **105**, 82, **2014**.
25. CHEN S., YANG J., ZHANG M., STRASSER R.J., SHENG Q. Classification and characteristics of heat tolerance in *Ageratina adenophora* populations using fast chlorophyll a fluorescence rise O-J-I-P. Environ. Exp. Bot., **122**, 126-140, **2016**.
26. EHLERINGER J. Ecophysiology of *Amaranthus palmeri*, a Sonoran Desert summer annual. Oecologia, **57**, 107, **1983**.
27. WARD S.M., WEBSTER T.M., STECKEL L.E. Palmer amaranth (*Amaranthus palmeri*): a review. Weed Technol., **27** (1), 12, **2013**.
28. GARVEY P.V., MEYERS S.L., MONKS D.W., COBLE H.D. Influence of Palmer amaranth (*Amaranthus palmeri*) on the critical period for weed control in plasticulture-grown tomato. Weed Technol., **27** (1), 165, **2016**.
29. KUMAR V., LIU R., BOYER G., STAHLMAN P.W. Confirmation of 2,4-D resistance and identification of multiple resistance in a Kansas Palmer amaranth (*Amaranthus palmeri*) population. Pest. Manag. Sci., **75**, 2925, **2019**.
30. KISTNER E.J., HATFIELD J.L. Potential geographic distribution of Palmer amaranth under current and future climates. Agric. Env. Lett., **3** (1), 2, **2018**.
31. Announcement on the release of the list of alien invasive species in China's natural ecosystem (the fourth batch), Available online: http://www.mee.gov.cn/gkml/hbb/bgg/201612/t20161226_373636.htm (accessed on 20 Dec. 2016).
32. CAO J.J., WANG R., LI Y.G., ZHANG G.F., GUO J.Y., WAN F.H. The phenotypic variation and environmental adaptability among different geographical opulations of *Amaranthus palmeri* in China. Plant Quarantine, **34** (3), 26, **2020**.
33. LI H., ZHAO L., ZHU P., ZHANG Y., ZHU G., LIU Q. Potential distribution of invasive Palmer amaranth in China (*Amaranthus palmeri*). J. Tianjin Norm. Univ. (Natural Science Edition), **35** (4), 0057, **2015**.
34. MO X.Q., MENG W., LI H.Y. New distribution records of three species of exotic plants in Tianjin: *Amaranthus palmeri*, *Ipomoea lacunosa* and *Aster subulatus*. J. Tianjin Norm. Univ. (Nat. Sci. Edn.), **37** (2), 36, **2017**.
35. WANG C.Y., WU B.D., JIANG K., ZHOU J.W. Differences in functional traits between invasive and native *Amaranthus* species under simulated acid deposition with a gradient of pH levels. Acta Oecol.-Int. J. Ecol., **89**, 32, **2018**.
36. WANG T.T., HAN J.H., FANG H.W., KHAN A.A., TANG L.L., ZHANG M., SHI F.C. The enhanced functional traits contribute to the successful invasion of *Amaranthus palmeri* in salinity environments: a comparison with its congeners. Biologia, **76** (9), 2455, **2021**.
37. SCHUTTE B.J., KLYPIN N., SHUKLA M.K. Influence of irrigation timing on disturbance-induced reductions in soil seedbank density. Weed Sci., **64** (4), 613, **2016**.
38. JIAN M.F., WANG S.C., YU H.P., LI L.Y., JIAN M.F., YU G.J. Fluorescence properties of submerged macrophytes in Nanjishan wetland, southern Poyang lake. J. Resour. Ecol., **6** (01), 52, 2015.
39. JIAN M.F., YANG Y.P., YU H.P., GONG Q.L., CHEN Y.L. Influences of different Cadmium concentration stress on chlorophyll and its photosynthetic fluorescence characteristics of Ramie (*Boehmeria nivea*). Acta Phytophysiol. Sin., **51** (8), 1331, **2015**.
40. NOWICKA B. Practical aspects of the measurements of non-photochemical chlorophyll fluorescence quenching in green microalgae *Chlamydomonas reinhardtii* using Open FluorCam. Physiol. Plant., **168** (3), 617, **2020**.
41. ORMEÑO E., OLIVIER R., MÉVY J.P., BALDY V., FERNABDEZ C. Compost may affect volatile and semi-volatile plant emissions through nitrogen supply and chlorophyll fluorescence. Chemosphere, **77** (1), 94. **2009**.
42. FLEXAS J., ESCALONA J.M., MEDRANO H. Water stress induces different levels of photosynthesis and electron transport rate regulation in grapevines. Plant Cell Environ., **22** (1), 39, **1999**.
43. DERKS A.K., BRUCE D. Rapid regulation of excitation energy in two pennate diatoms from contrasting light climates. Photosynth. Res., **138** (2), 149, **2018**.
44. SUN Y.J., WANG J.H., GENG Q.W., XING H., ZHAI H., DU Y.P. Effects of different concentrations of ozone stress on photosynthetic system II in *Vitis vinifera* cv. 'Cabernet Sauvignon'. Acta Phytophysiol. Sin., **51** (11), 1947, **2015**.
45. LU P., LI J., JIN C., JIANG B.W., BAI Y. Different growth responses of an invasive weed and a native crop to nitrogen pulse and competition. PLoS One, **11** (6), 3, **2016**.
46. AERTS R., BERENDSE F., SCHMITZ C.M. Competition in heathland along an experimental gradient of nutrient availability. Oikos, **57** (3), 313, **1990**.
47. KOŁODZIEJEK J. Growth and competitive interaction between seedlings of an invasive Rumex confertus and of co-occurring two native Rumex species in relation to nutrient availability. Sci Rep, **9** (1), 3298, **2019**.
48. WU C., WANG Z.Q., SUN H.L., GUO S.L. Effects of different concentrations of nitrogen and phosphorus on chlorophyll biosynthesis, chlorophyll a fluorescence, and photosynthetic rate in *Larix olgensis* seedlings. Sci. Silv. Sin., **44** (4), 031, **2005**.
49. CAI M.L., ZHANG Q.L., ZHENG X.T., ZHAI J.J., PENG C.L. Comparison of leaves and stems of *Paederia scandens* (lour.) merr. in tolerance to low temperature. Photosynthetica, **58** (3), 846, **2020**.
50. LONG S.P. Environmental responses, in: R.F. Sage, R.K. Monson (Eds.), C_4 Plant Biology. Academic Press, San Diego, pp. 215, **1999**.
51. GUO P., AL-KHATIB K. Temperature effects on germination and growth of redroot pigweed (*Amaranthus retroflexus*), Palmer amaranth (*A. palmeri*),

and commonwaterhemp (*A. rudis*). Weed Sci., **51** (6), 869, **2003**.

52. GONG Z.N., FAN Y.B., LIU H., ZHAO W.J. Chlorophyll fluorescence response characteristics of typical emergent plants under different total nitrogen gradient. Chin. Bull. Bot., **51** (5), 631, **2016**.
53. XIN X.L., QIN S.W., ZHANG J.B., ZHU A.N., YANG W.L., ZHANG X.F. Yield, phosphorus use efficiency and balance response to substituting long-term chemical fertilizer use with organic manure in a wheat-maize system. Field Crop. Res., **208**, 27, **2017**.
54. ZHENG Z.B., GAO S., WANG G.C. Far red light induces the expression of LHCSR to trigger nonphotochemical quenching in the intertidal green macroalgae *Ulva prolifera*. Algal Res., **40** (1), 101512, **2019**.
55. HUNER N.P.A., OQUIST G., SARHAN F. Energy balance and acclimation to light and cold. Trends Plant Sci., **3** (6), 224, **1998**.
56. VLČKOVÁ, A., ŠPUNDOVÁ, M., KOTABOVÁ, E., NOVOTNY, R., DOLEŽAL K., NAUŠ J. Protective cytokinin action switches to damaging during senescence of detached wheat leaves in continuous light. Physiol. Plant., **126** (2), 257, **2010**.
57. TANG G., LI X., LIN L., GUO H. Combined effects of girdling and leaf removal on fluorescence characteristic of *Alhagi sparsifolia* leaf senescence. Plant Biol., **17** (5), 980, **2015**.
58. AKRAMA M., ASHRAFB M.Y., JAMILA M., IQBALA R.M., NAFEESA M., KHANA M.A. Nitrogen application improves gas exchange characteristics and chlorophyll fluorescence in maize hybrids under salinity conditions. Russ. J. Plant Physiol., **58** (3), 398, **2011**.
59. WANG C.Y., ZHOU J.W., LIU J., JIANG K. Differences in functional traits between invasive and native *Amaranthus* species under different forms of N deposition. Sci. Nat., **104**, 7, **2017**.
60. KHANGURA R.S., JOHAL G.S., DILKES B.P. Variation in maize chlorophyll biosynthesis alters plant architecture. Plant Physiol., **184** (1), 300, **2020**.
61. BERGER S.T., FERRELL J.A., ROWLAND D.L., WEBSTER T.M. Palmer Amaranth (*Amaranthus palmeri*) competition for water in cotton. Weed Sci. **63** (4)**,** 935, **2015**.
62. DENG J.L. Gray prediction and decision making. Huazhong University of Science and Technology Press, Wuhan, pp. 10, **1986**.
63. WANG C.Y., ZHOU J.W., LIU J.L., DU D.L. Responses of soil N-fixing bacteria communities to invasive species over a gradient of simulated nitrogen deposition. Ecol. Eng., **98**, 32, **2017**.
64. TIAN B., RAN X.Q., XUE H., XIE J., CHEN B., WU Y.X., WANG J.F., WANG X. Evaluation of the nutritive value of 42 kinds of forage in Guizhou Province by gray relational grade analysis. Acta Pratac. Sin., **23** (1), 92, **2014**.