



Compensatory light utilization of *Phalaris arundinacea* within the *Phalaris arundinacea*–*Phragmites australis* compound community

Yun Zhao, Weiguo Fu, Pingping Li, Ke Xue, Yuxuan Wang & De Ke Xing

To cite this article: Yun Zhao, Weiguo Fu, Pingping Li, Ke Xue, Yuxuan Wang & De Ke Xing (2018) Compensatory light utilization of *Phalaris arundinacea* within the *Phalaris arundinacea*–*Phragmites australis* compound community, Journal of Plant Interactions, 13:1, 280–287, DOI: [10.1080/17429145.2018.1474392](https://doi.org/10.1080/17429145.2018.1474392)

To link to this article: <https://doi.org/10.1080/17429145.2018.1474392>



© 2018 The Author(s). Published by Informa UK Limited, trading as Taylor & Francis Group



Published online: 14 May 2018.



Submit your article to this journal [↗](#)



Article views: 426



View related articles [↗](#)



View Crossmark data [↗](#)



Citing articles: 1 View citing articles [↗](#)

RESEARCH ARTICLE



Compensatory light utilization of *Phalaris arundinacea* within the *Phalaris arundinacea*–*Phragmites australis* compound community

Yun Zhao^a, Weiguo Fu^{a,b}, Pingping Li^b, Ke Xue^a, Yuxuan Wang^a and De Ke Xing^a

^aKey laboratory of Modern Agricultural Equipment and Technology, Ministry of Education & Jiangsu Province, Jiangsu University, Zhenjiang, People's Republic of China; ^bCooperative Innovation Center of Southern Modern Forestry, Nanjing Forestry University, Nanjing, People's Republic of China

ABSTRACT

This study investigated the light utilization characteristics of *Phalaris arundinacea* within the *Phalaris arundinacea*–*Phragmites australis* compound community. The investigation was based on the response curve equation of the net photosynthetic rate–photosynthetic photon flux density (Pn–PPFD) of *P. arundinacea* and on the distribution of PPFD on the surface canopy of *P. arundinacea* within the compound community. Results showed that *P. arundinacea* was able to compensate for substantial reduction in available light, and utilize the weak light within the lower part of the compound community. On the one hand, the density of *P. australis* within the compound community determined the compensatory light utilization rate (CLUR) of *P. arundinacea*. On the other hand, the CLUR amplitude of *P. arundinacea* within the compound community with the same *P. australis* density was relatively small in a day. The results can help people to regulate *P. arundinacea*–*P. australis* compound communities to maintain a long-term, stable coexistence in the constructed wetlands.

Abbreviations: CK – control; CLUR, compensatory light utilization rate; LER, light extinction rates; Pn, net photosynthetic rate; PPFD, photosynthetic photon flux density.

ARTICLE HISTORY

Received 28 November 2017
Accepted 5 May 2018

KEYWORDS

Density; compensatory light utilization; light response curve; *Phalaris arundinacea*; *Phragmites australis*

Introduction

Phalaris arundinacea and *Phragmites australis*, which possess highly similar biological characteristics, are perennial rhizome clonal plants that often live in wetlands such as river/lake floods, low-lying lands, swamps, and coasts. *P. arundinacea* is widely distributed in the north temperate zone of North America, Europe, and Asia (Martina and Ende 2012; Martínková and Klimešová 2017), whereas *P. australis* is widely distributed almost all over the world (Tucker 1990; Elonger 2009; Kulmatiski et al. 2011). In Europe, *P. arundinacea* and *P. australis* are widely used to build constructed wetland plant communities due to their extremely strong decontamination effects (Vymazal and Kröpfelová 2005; Gagnon et al. 2010; Vymazal 2011; Pedescoll et al. 2015). Jan Vymazal evaluated the establishment after planting, seasonal/long-term growth, and growth characteristics (biomass, stem count, and stem length) for *P. australis* and *P. arundinacea* planted in constructed wetlands for wastewater treatment in the Czech Republic (Vymazal and Kröpfelová 2005). Recently, Brezinová and Vymazal have evaluated the accumulation of heavy metals in above-ground biomass of *P. australis* and *P. arundinacea* in horizontal flow constructed wetlands for wastewater treatment (Březinová and Vymazal 2015; Vymazal and Březinová 2016). However, both *P. arundinacea* and *P. australis* are very competitive, and these plants often develop into the mono-dominant population in the natural ecological community by inhibiting the growth of other species (Adams and Galatowitsch 2005; Perkins and Wilson 2005; Kercher et al. 2007; Rodriguez and Brisson 2015).

These two species in North America were even considered invasive species and subsequently controlled by humans (Herr-Turoff and Zedler 2007; Bains et al. 2009; Uddin et al. 2012). In the twentieth century, *P. arundinacea* considerably increased its range in North America, becoming an invasive weed in many wetlands. As such, this species has been officially identified as a pest in nine American states (Lavergne and Molofsky 2004; Herr-Turoff and Zedler 2007). The distribution and abundance of *P. australis* in North America have dramatically increased over the past 150 years. The introduction of a non-native genotype of the common reed from other areas is reportedly responsible for the invasive characteristic of *P. australis* in North America (Salt-onstall 2002). However, the two species with such strong competitive abilities are often chosen as dominant species and planted in the same constructed wetland which often operates for a long time, what will happen to the plant community in the constructed wetland?. Some studies reported that *P. australis* displaces *P. arundinacea*, although this phenomenon inconsistently occurs in systems where both plants are present (Vymazal and Kröpfelová 2005); even so, the displacement of *P. arundinacea* by *P. australis* takes a long time (Březinová and Vymazal 2014). Other studies reported that the two species in the Zhenjiang Waterfront Wetland in the lower reaches of Yangtze River in China could maintain a long-term and stable coexistence (Fu et al. 2011). Scholars have tried to elucidate the mechanisms underlying the long-term stable coexistence between the two species both in constructed and natural wetlands.

CONTACT Weiguo Fu  fuweiguo@ujs.edu.cn

Considering the extremely low light compensation point ($46 \mu\text{mol m}^{-2} \text{s}^{-1}$) of *P. arundinacea*, this author previously concluded that *P. arundinacea* could compensate for substantial reduction in available light, and make use of the weak light within the lower part of the *P. arundinacea*–*P. australis* compound community, which can alleviate the competition between the two species for the light resource (Fu et al. 2011). Břzinová and Vymazal evidently concur with this conclusion (Břzinová and Vymazal 2014).

Nevertheless, systematic and quantitative studies have yet not determine the compensatory light utilization rate (CLUR) of *P. arundinacea* within various *P. arundinacea*–*P. australis* compound communities with different densities of *P. australis*. In the present paper, based on the Pn-PPFD response curve fitting equation of *P. arundinacea* and the distribution of PPFD on the surface canopy of *P. arundinacea* population within those *P. arundinacea*–*P. australis* compound communities with three typical densities of *P. australis* found in the Zhenjiang Waterfront Wetland in the lower reaches of Yangtze River, this study measured the CLUR of *P. arundinacea* within such *P. arundinacea*–*P. australis* compound communities and identified a maintenance mechanism for the two species to obtain a relatively stable coexistence pattern with respect to the comprehensive utilization of light energy. On the basis of the above mechanism and on other work suggesting that a metapopulation could achieve stable coexistence through population management (Hastings 2003; Dushoff 2004), the *P. australis*–*P. arundinacea* compound community in the constructed wetlands could be regulated to maintain a long-term, stable coexistence between the two species.

Materials and methods

Study site and study species

The Zhenjiang Waterfront Wetland ($32^{\circ}15'N$ and $119^{\circ}28'E$) is a 5000-ha intermittent river wetland along the Yangtze River that lies to the north of Zhenjiang City. The Zhenjiang Waterfront Wetland formed from the accumulation of massive silt deposits in the Yangtze River. The primary succession of the plant community in the wetland occurred with gradual elevation of the wetland beach. The vegetation in the wetland has successively passed through three community types over its succession process, namely, an initial community of *P. arundinacea*, an intermediate transitional community of *P. arundinacea*–*P. australis*, and a climax community *P. australis*. The *P. arundinacea*–*P. australis* transitional community took the longest time in the whole succession process, accounting for more than 50% of the total succession process time. During the succession process, the *P. australis* population gradually displaced the *P. arundinacea* population through an increase in the density of *P. australis*. This condition provides the ideal experimental material for us to study the compensatory light utilization characteristics of *P. arundinacea* within the *P. arundinacea*–*P. australis* compound community with different densities of *P. australis*.

Material selection

In the Zhenjiang Waterfront Wetlands in the lower reaches of Yangtze River, *P. arundinacea* often germinates in the beginning of February and matures by the end of May,

with a growth period of about 130 days. Meanwhile, *P. australis* often germinates in mid-March and matures by the end of October, with a growth period of about 220 days. The two species have an overlap of about 80 days during the growth process (Fu et al. 2011). Experiments were performed on early May 2016, in which the plant heights of *P. australis* and *P. arundinacea* were about 3.0 and 1.5 m, respectively, and the shade effect of *P. australis* on *P. arundinacea* was most obvious. First, some *P. arundinacea* individuals from the *P. arundinacea* community that were not shaded by *P. australis* in the wetlands were chosen to study the Pn-PPFD response curve fitting equations of *P. arundinacea* at different time points in a day. Thereafter, three *P. arundinacea*–*P. australis* compound communities with *P. australis* densities of about 25, 35, and 45 shoot counts m^{-2} were selected to measure the photosynthetic photon flux density (PPFD) on the surface canopy of *P. arundinacea* within the lower part of the *P. arundinacea*–*P. australis* compound community having the three aforementioned densities of *P. australis*. Those three *P. australis* densities represent the different developmental stages of the *P. arundinacea*–*P. australis* compound communities, namely, (1) the semi-mature, (2) middle and late, and (3) the near-mature stages, respectively. The maximum density of the *P. australis* community at the fully mature stage is about 50 shoot counts m^{-2} in this wetland.

Pn-PPFD response curve equations

Measurements were conducted on a clear day (May 5). The third fully expanded leaf from the top of three uniform and vigorous individuals (as three repetitions) of *P. arundinacea* from the *P. arundinacea* community were chosen. The net photosynthetic rate -photosynthetic photon flux density (Pn)-PPFD response curve was measured once every 2 h from 8:00 to 16:00 using a LI-6400 Portable Photosynthesis System (LI-COR6400, USA). The Pn-PPFD response curves of *P. arundinacea* were determined across a PPFD coverage range of $0\text{--}2500 \mu\text{mol m}^{-2} \text{s}^{-1}$ using a light emitting diode (LED) light source and under ambient CO_2 concentrations. Thereafter, the optimal Pn-PPFD response curve equations of *P. arundinacea* at different time points were obtained.

Light extinction rates

With the ST285 automatic range illuminometer (produced by the Photoelectric Instrument Factory of Beijing Normal University), the PPFD on the surface canopy of *P. arundinacea* within the *P. arundinacea*–*P. australis* compound communities with three densities of *P. australis* were measured and abbreviated as PPFD' at 8:00, 10:00, 12:00, 14:00, and 16:00 on May 5. The PPFD on the surface canopy of *P. arundinacea* within the *P. arundinacea* community that was not under the shade of *P. australis* was also measured simultaneously and abbreviated as PPFD_{max}. Ten values of PPFD for every surface canopy were recorded, and then the mean values were obtained. The light extinction rates (LERs) caused by the shade of the *P. australis* populations on the *P. arundinacea* populations at different time points were calculated as $\text{LER \%} = (1 - \text{PPFD}' / \text{PPFD}_{\text{max}}) \times 100$.

Compensatory light utilization rate

With PPFD on the surface canopy of *P. arundinacea* within the compound community as an independent variable, the forecast values of P_n (independent variable of PPFD) and $P_{n_{max}}$ (independent variable of PPFD_{max}) of *P. arundinacea* at the different measurement time points were obtained on the basis of the P_n -PPFD response curve fitting equations of *P. arundinacea* at the corresponding measurement time points. The CLURs of *P. arundinacea* within the *P. arundinacea*-*P. australis* compound community were calculated as $CLUR \% = P_n/P_{n_{max}} \times 100$.

With this method, the CLURs of *P. arundinacea* within the *P. arundinacea*-*P. australis* compound communities with the three densities of *P. australis* at the different time points in a day were obtained.

Statistical analysis

We analyzed LERs and CLURs of *P. arundinacea* in the communities among the three densities of *P. australis* using repeated measures analysis of variance (rmANOVA). For the data of LERs and CLURs analyses, the mean \pm S.E. were reported and the SPSS 17.0 statistical software was used by one-way ANOVA. LSD multiple comparison test was used at $\alpha = 0.05$.

Results

Pn-PPFD response curve and its fitting equation of *P. arundinacea*

The P_n -PPFD response curves of *P. arundinacea* at 8:00, 10:00, 12:00, 14:00, and 16:00 were obtained on the same day by using a LI-6400 Portable Photosynthesis System. The curves are plotted in Figure 1(A,B,C,D,E), respectively. The P_n -PPFD response curves of *P. arundinacea* showed similar trends among the five measurement time points. With increasing PPFD, P_n initially increased rapidly and then gradually peaked before gradually decreasing, and the P_n -PPFD response curves of *P. arundinacea* at all measurement time points showed a parabolic trend, which is suitable for fitting with quadratic function equations. The coefficient of determination (R^2) of the fitting equation at each measurement time point was more than 0.94 (Table 1), which showed that a satisfactory fit resulted. Therefore, the corresponding P_n of *P. arundinacea* at any PPFD (within the range of the fitted PPFD) could be calculated on the basis of the above P_n -PPFD response curve fitting equations.

Table 1. P_n -PPFD response curve fitting equation of *P. arundinacea* at different measurement time points.

| Measurement time point | Fitting equation | Coefficient of determination (R^2) |
|------------------------|---|--|
| 8:00 | $Y = -5 \times 10^{-6}X^2 + 0.0150X + 1.5636$ | 0.9438 |
| 10:00 | $Y = -4 \times 10^{-6}X^2 + 0.0147X + 1.3829$ | 0.9415 |
| 12:00 | $Y = -4 \times 10^{-6}X^2 + 0.0136X + 1.2515$ | 0.9465 |
| 14:00 | $Y = -4 \times 10^{-6}X^2 + 0.0124X + 1.2094$ | 0.9473 |
| 16:00 | $Y = -6 \times 10^{-6}X^2 + 0.0176X + 1.2854$ | 0.9486 |

Note: X stands for the PPFD on the surface canopy of *P. arundinacea*, whereas Y stands for the forecast value of P_n to the corresponding PPFD.

Distribution of PPFD on the surface canopy of *P. arundinacea* and its LER

The daily dynamics of the PPFD on the surface canopy of *P. arundinacea* growing in different environments are shown in Figure 2. All PPFD values showed single-peak curves, with peak values appearing at 12:00. However, the decline in PPFD on the surface canopy of *P. arundinacea* among the *P. arundinacea*-*P. australis* compound communities with the three densities of *P. australis* was considerably different from that on the surface canopy of *P. arundinacea* within the *P. arundinacea* community not under the shade of *P. australis*. The largest decline in daily average PPFD occurred within the compound community with a *P. australis* density of 45 shoot counts m^{-2} , with a decline of 82.4%. The daily average PPFDs of the communities with *P. australis* densities of 35 and 25 shoot counts m^{-2} declined by 55.3% and 45.4%, respectively.

Figure 3 shows the LER caused by the shade of the *P. australis* populations on the *P. arundinacea* populations within the *P. arundinacea*-*P. australis* compound communities at the different measurement time points during the day. As shown by Figure 4, the LERs on the surface canopy of *P. arundinacea* within the *P. arundinacea*-*P. australis* compound communities increased to varying degrees along with the increase in the density of *P. australis*. When the densities of *P. australis* were 25, 35, and 45 shoot counts m^{-2} within the *P. arundinacea*-*P. australis* compound communities, the variation ranges of LER in a day were 41.11%–47.81%, 51.36%–56.50%, and 80.78%–83.39%, respectively. Statistical analysis showed that the LERs on the surface canopy of *P. arundinacea* within the compound community with a *P. australis* density of 45 shoot counts m^{-2} were significantly greater than those on the surface canopy of *P. arundinacea* within the compound community with *P. australis* densities of 25 ($p = 0.016, 0.018, 0.019, 0.016$ and 0.021 at 8:00, 10:00, 12:00, 14:00, and 16:00, respectively) and 35 ($p = 0.032, 0.038, 0.041, 0.043,$ and 0.047 at 8:00, 10:00, 12:00, 14:00, and 16:00, respectively) shoot counts m^{-2} at each measurement time point; however, no significant differences in LERs were found between the two compound communities with *P. australis* densities of 25 and 35 shoot counts m^{-2} at each measurement time point ($p = 0.082, 0.094, 0.092, 0.066,$ and 0.071 at 8:00, 10:00, 12:00, 14:00, and 16:00, respectively) of the day. In addition, no significant differences in LER were observed among the different time points in a day within the compound community having the same *P. australis* density (all $p > 0.05$).

CLURs of *P. arundinacea* within the compound community

The daily P_n dynamics of the surface canopy leaf of *P. arundinacea* growing in the different environments are shown in Figure 4. Similar to those of PPFD, the daily dynamics of the P_n of the surface canopy leaf of *P. arundinacea* growing in the different environments were all single-peak curves, although the peak values appeared at 10:00, one hour earlier than the appearance of PPFD peak values. With an increase in the density of *P. australis* within the compound community, the leaf P_n of *P. arundinacea* decreased to varying degrees at the same measurement time point in a day. As compared with that of the leaf of *P. arundinacea* within the *P. arundinacea*

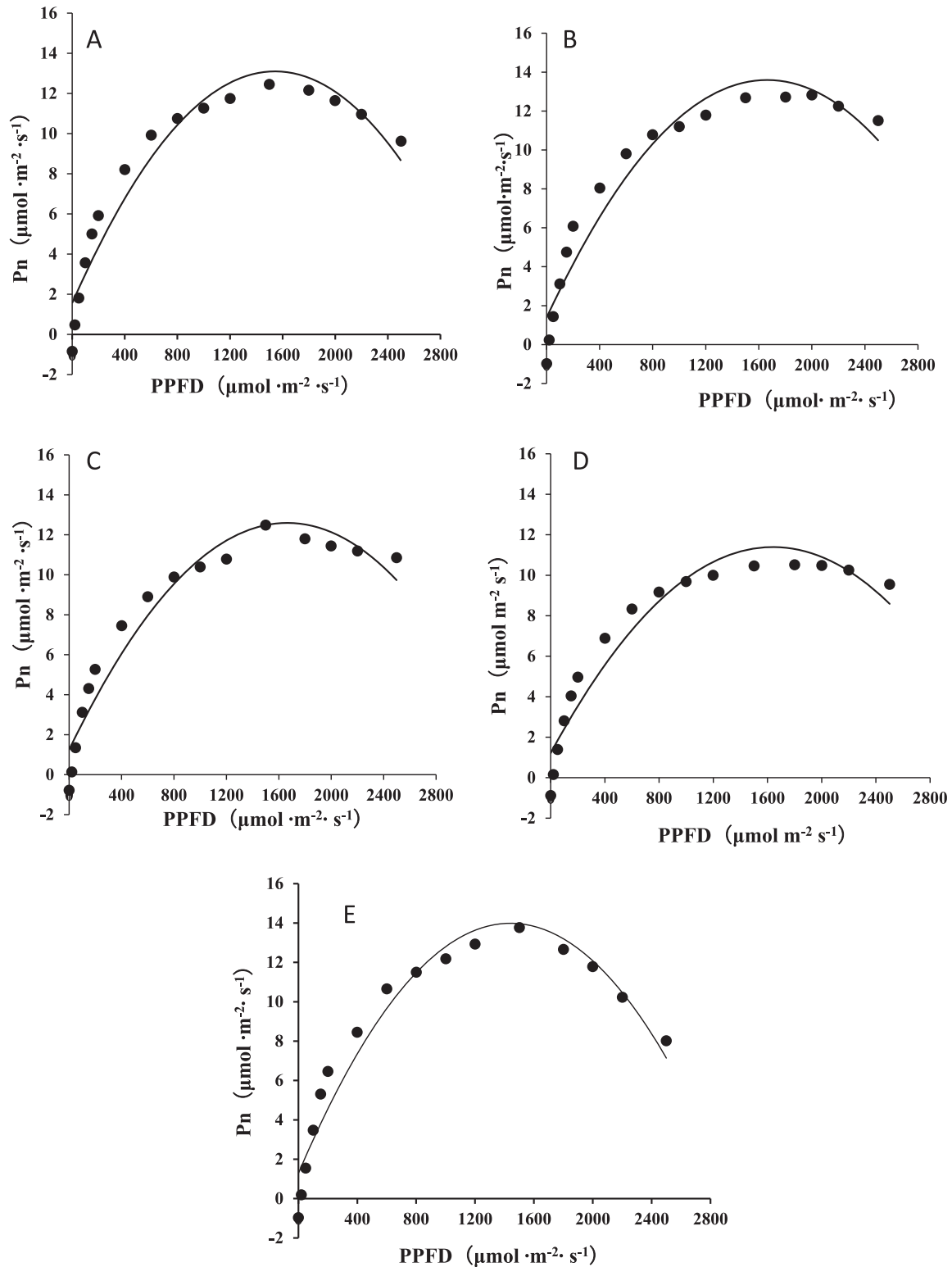


Figure 1. Pn-PPFD response curves of *P. arundinacea* at different measurement time points. A, B, C, D, and E represent the Pn-PPFD response curves of *P. arundinacea* at 8: 00, 10: 00, 12: 00, 14:00, and 16:00, respectively. Pn-net photosynthetic rate; PPFD-photosynthetic photon flux density.

community not being shaded by *P. australis*, the daily average leaf Pn of *P. arundinacea* within the compound communities with *P. australis* densities of 25, 35, and 45 shoot counts m^{-2} declined by 25.3%, 33.5%, and 63.7%, respectively.

The CLURs of *P. arundinacea* within the compound communities at different time points in a day are shown in Figure 5. The CLURs of *P. arundinacea* within the compound communities decreased to varying degrees with an increase in the density of *P. australis*. When the densities of *P. australis* were 25, 35, and 45 shoot counts m^{-2} within the compound

communities, the daily average CLURs of *P. arundinacea* were 74.72%, 66.43%, and 36.18%, respectively; the daily CLUR variation ranged from 70.36% to 79.89%, 63.01% to 68.99%, and 33.27% to 39.98%, respectively; and the corresponding CLURs amplitudes were 9.53%, 5.98%, and 6.71%, respectively. The amplitude of the CLURs of *P. arundinacea* within the compound community with the same *P. australis* density was relatively small during the day. Statistical analysis showed that the CLURs of *P. arundinacea* within the compound community with a *P. australis* density of 45

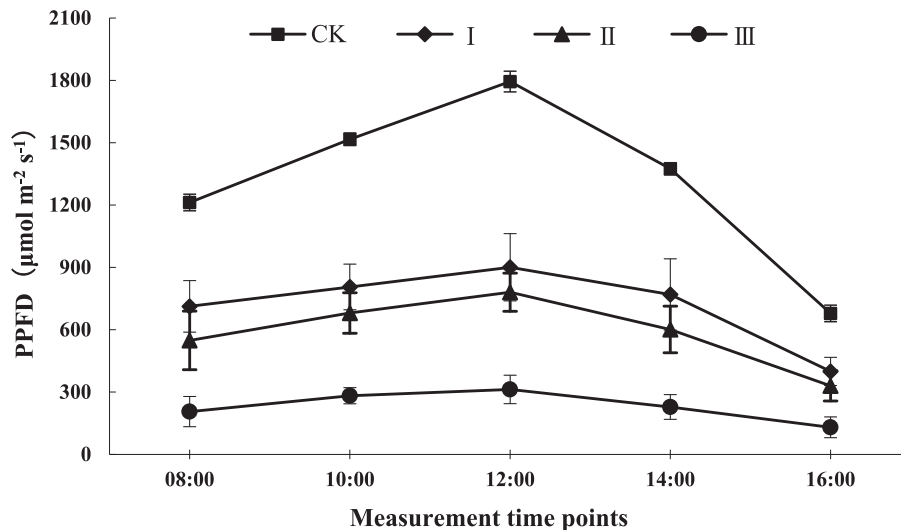


Figure 2. Daily dynamics of the PPFD on the surface canopy of *P. arundinacea* growing in different environments. Roman numerals I, II, and III stand for the PPFD on the surface canopy of *P. arundinacea* within the *P. arundinacea*–*P. australis* compound communities with *P. australis* densities of 25, 35, and 45 shoot counts m^{-2} , respectively. CK refers to the surface canopy of *P. arundinacea* within the *P. arundinacea* community not being shaded by *P. australis*. The bar indicates the standard deviation, $n = 10$. PPFD–photosynthetic photon flux density.

shoot counts m^{-2} were significantly less than those of *P. arundinacea* within the compound community with *P. australis* densities of 25 ($p = 0.017, 0.019, 0.022, 0.013, \text{ and } 0.012$ at 8:00, 10:00, 12:00, 14:00, and 16:00, respectively) and 35 ($p = 0.033, 0.038, 0.041, 0.032, \text{ and } 0.036$ at 8:00, 10:00, 12:00, 14:00, and 16:00, respectively) shoot counts m^{-2} at each measurement time point. However, no significant differences in CLUR were found between the two compound communities with *P. australis* densities of 25 and 35 shoot counts m^{-2} at each measurement time points ($p = 0.087, 0.091, 0.092, 0.062, \text{ and } 0.089$ at 8:00, 10:00, 12:00, 14:00, and 16:00, respectively) in a day. Finally, statistical analysis showed no significant differences in CLUR among the different measurement time points in a day within the compound community having the same *P. australis* density (all $p > 0.05$).

Discussion

Relationship between the CLUR of *P. arundinacea* and the density of *P. australis* within the compound community

The characteristic of compensatory light utilization is prevalent in plant species possessing a very low light compensation point, and it not only often affects the vertical distribution patterns of plant species in some compound communities (Xue et al. 2008; Wang et al. 2015), but is also widely used to guide the stereoscopic cultivation of crops in agriculture (Lou et al. 2014; Wang et al. 2015). However, it is the density of plant species occupying the upper space in the compound community that ultimately determines the CLUR of plant species possessing very low light compensation points and occupying the lower space in the compound community. In the present paper, by varying the distribution of PPFD on the surface canopy of *P. arundinacea* and the subsequent Pn of *P. arundinacea*, we found that the density of *P. australis* determined the CLUR of *P. arundinacea* in the *P. arundinacea*–*P. australis* compound community. The CLUR of *P. arundinacea* decreased to varying degrees with an increase in the density of *P. australis* within the compound community. However, the downward trend in the CLUR of

P. arundinacea did not decrease uniformly. At first the CLUR decreased slowly; only when the density of *P. australis* reached a certain threshold did the CLUR of *P. arundinacea* within the compound community sharply decrease. This explains the phenomena that accelerated displacement of *P. arundinacea* population by *P. australis* population appeared in the later stage of population displacement in some natural wetlands (Fu et al. 2007) and constructed wetlands (Březinová and Vymazal 2014).

Relationship between the regulation of plant community and the density of *P. australis* in the constructed wetland

Another study showed that *P. australis* tended to displace *P. arundinacea* in some constructed wetlands, although this phenomenon inconsistently occurred in systems where both plants were present (Vymazal and Kröpfelová 2005). We note that Vymazal and Kröpfelová did not mention the density of *P. australis*, so it's reasonable to suspect that the inconsistencies in observed plant displacement were due to the difference in the densities of *P. australis* within the *P. arundinacea*–*P. australis* compound community among the different constructed wetlands. On the basis of the above results, we can deduce that some moderate or greater density of *P. australis* must exist, and the CLUR of *P. arundinacea* is high enough to maintain its healthy growth within the *P. arundinacea*–*P. australis* compound community. In the present study, when the densities of *P. australis* within the compound communities were 25 and 35 shoot counts m^{-2} , the CLURs of *P. arundinacea* still maintained high levels with 74.72% and 66.43%, respectively. On the basis of the growth of *P. arundinacea*, *P. arundinacea* within the compound communities with the above two densities of *P. australis* were able to maintain healthy or relatively healthy growth conditions. In addition, during the course of the study, *P. arundinacea* was in the later grain-filling period.

Therefore, the shade resulting from *P. australis* can exert a certain degree of adverse impact on its grain filling; however, for a cloned plant such as *P. arundinacea* whose main mode

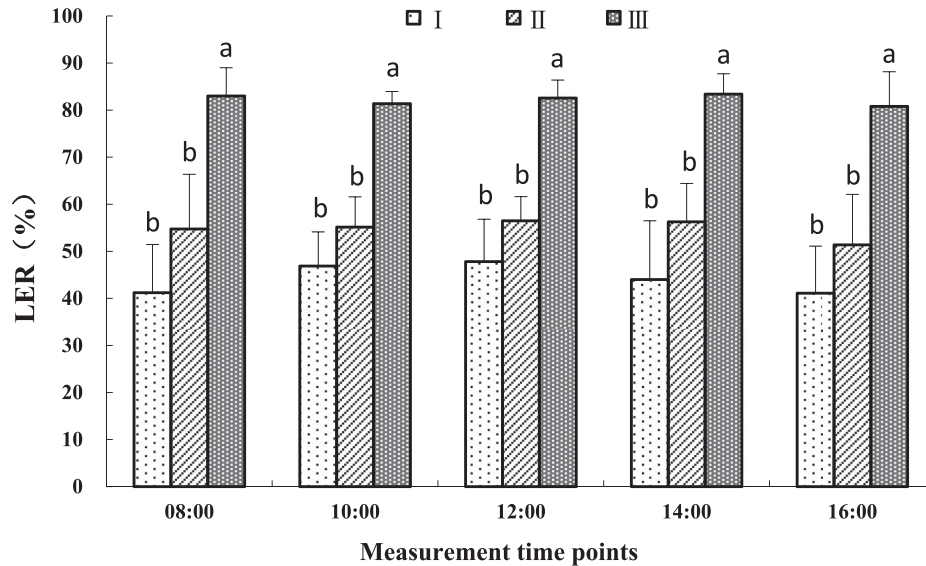


Figure 3. LER caused by the shade of the *P. australis* populations on the *P. arundinacea* populations at different time points in a day. Roman numerals I, II, and III stand for the *P. arundinacea*–*P. australis* compound communities with *P. australis* densities of 25, 35, and 45 shoot counts m^{-2} , respectively. CK refers to the *P. arundinacea* community not being shaded by *P. australis*. Error bars are \pm standard error, $n = 10$. PPFD-photosynthetic photon flux density.

of reproduction is rhizome propagation rather than seed propagation (Martina and Ende 2013; Chen et al. 2014; Martínková and Klimešová 2017), the aforementioned adverse impact on its grain filling will not significantly affect the normal growth and development of the *P. arundinacea* population. By contrast, when the density of *P. australis* within the compound communities rose to 45 shoot counts m^{-2} , the CLUR of *P. arundinacea* fell to as low as 36.18%. Furthermore, *P. arundinacea* individuals within the compound community were no longer able to maintain healthy or even relatively healthy growth conditions, and some growth stress traits, such as the yellow leaves, thin stems, low density, and few branches, generally occurred. Therefore, the density of *P. australis* within the compound community should be controlled at 35 shoot counts m^{-2} or slightly higher but must not reach 45 shoot counts m^{-2} to maintain the stable coexistence of the two species in the *P. arundinacea*–*P. australis*

compound community in the Zhenjiang Waterfront Wetland of the lower reaches of the Yangtze River. However, this recommended density of *P. australis* applies only to constructed wetlands where the cultivar of planted *P. australis* must be the same as that of *P. australis* growing in the Zhenjiang Waterfront Wetland. In the studied wetland, the maximum density of the *P. australis* community at the fully mature stage was only about 50 shoot counts m^{-2} , while the density of *P. australis* planted in the some constructed wetlands in Europe ranged from 11 to 332 (Vymazal and Kröpfungová 2005). The huge difference in the density of *P. australis* in the different regions mainly resulted from the difference in the cultivars of planted *P. australis*. Therefore, the difference in cultivars should be taken into account when the appropriate density of *P. australis* maintaining a stable *P. arundinacea*–*P. australis* compound community in the constructed wetlands is recommended. In addition, studies have shown that

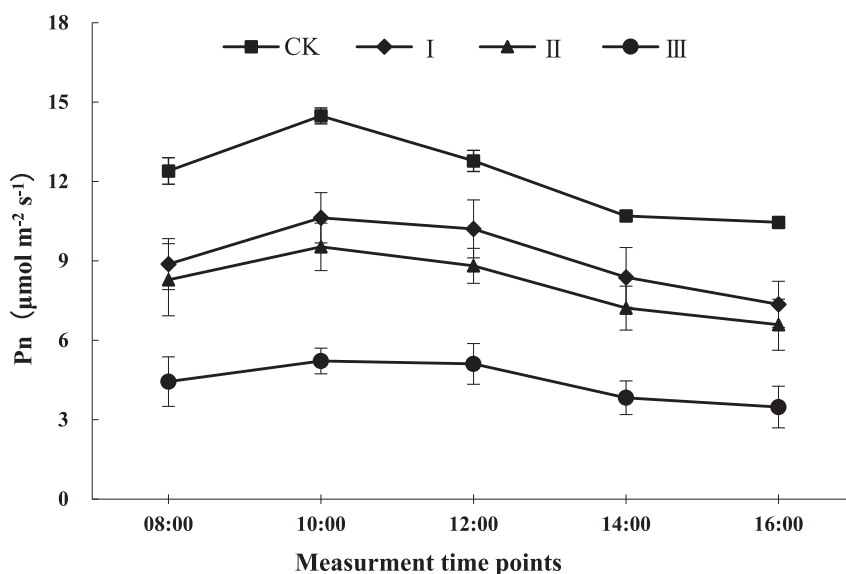


Figure 4. LERs caused by the shade of the *P. australis* populations on the *P. arundinacea* populations at different time points in a day. Roman numerals I, II, and III stand for the *P. arundinacea*–*P. australis* compound communities with *P. australis* densities of 25, 35, and 45 shoot counts m^{-2} , respectively. Different small letters indicate significant difference between the communities with three densities of *P. australis* according to LSD test ($p < 0.05$). Error bars are \pm standard error. LER-light extinction rates.

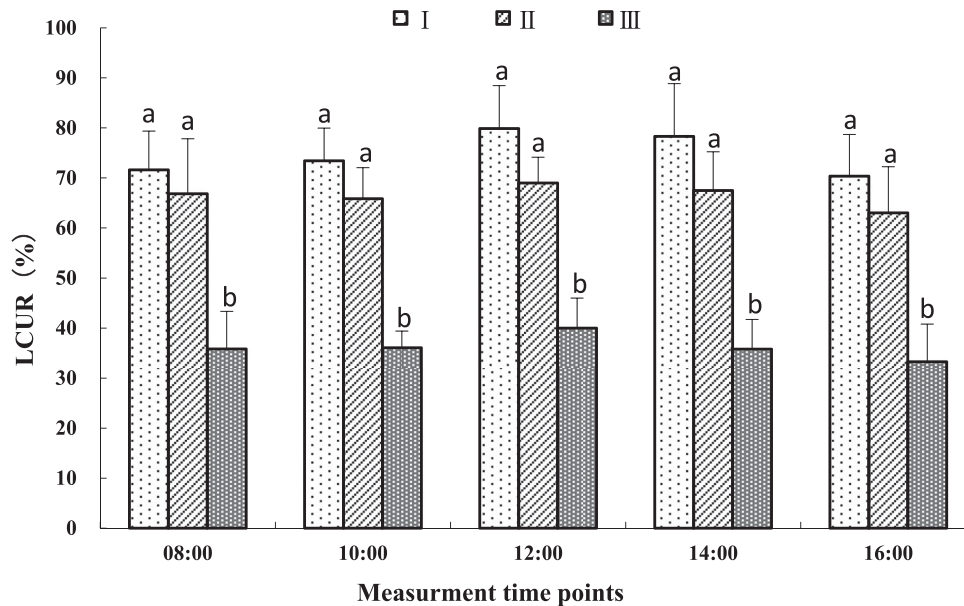


Figure 5. Compensatory light utilization rates (CLURs) of *P. arundinacea* within the compound communities at different time points in a day. Roman numerals I, II, and III stand for the *P. arundinacea*–*P. australis* compound communities with *P. australis* densities of 25, 35, and 45 shoot counts m^{-2} , respectively. Different small letters indicate significant difference between the communities with three densities of *P. australis* according to LSD test ($p < 0.05$). Error bars are \pm standard error. CLUR- compensatory light utilization rate.

lowering light availability with a cover crop in restored prairie pothole wetlands might slow *P. Arundinacea* invasion in some regions where *P. arundinacea* was regarded as an invasive species, but its effect is extremely limited (Perry and Galatowitsch 2004, 2006), and this outcome is precisely due to the characteristic of the compensatory light utilization of *P. arundinacea*.

Other factors affecting the stable coexistence of *P. arundinacea* and *P. australis* in the compound community

The growth and development of plants are influenced by plant-intrinsic factors and external environmental factors. Likewise, the stable coexistence of *P. arundinacea* and *P. australis* in the Zhenjiang Waterfront Wetland must be the result of the combined effect of many factors, including the density effect of *P. australis*. In addition to the density effect of *P. australis*, many other obvious differences were observed between the two species, including the growth period, plant height, light compensation point, and root depth (Lavergne and Molofsky 2006; Zhang and Luo 2008; Fu et al. 2011; Ge et al. 2011; Nelson and Anderson 2015). In particular, Fu Weiguo suggested that despite the stronger competitiveness of *P. australis* compared with *P. arundinacea*, the latter's earlier germination of about 30 days resulting from the difference in growth period may have allowed this species to establish rapidly and preempt the establishment of *P. australis*, and the absence of shading by *P. australis* would also have been very beneficial for the early growth of *P. arundinacea* during this period (Herr-Turoff and Zedler 2007; Fu et al. 2011). In addition, some scholars have pointed out that an obvious niche segregation exists between the two species, which could reduce the interspecific competition and promote the sharing of various resources between them (Fu et al. 2015). This paper suggests a maintenance mechanism by which the two plant species can achieve a relatively stable coexistence, by considering the density effect of *P. australis*

on the ability of *P. arundinacea* to compensate for reduced light levels.

Conclusion

P. arundinacea can compensate for reduced light and make use of the weak light within the lower part of the *P. arundinacea*–*P. australis* compound community, provided that there are reasonable limits on the density of *P. australis*. The density of *P. australis* within the compound community determined the CLUR of *P. arundinacea*. In addition, the amplitude of the CLURs of *P. arundinacea* within the compound community with the same *P. australis* density was relatively small during the day. This result indicates that the compensatory light utilization of *P. arundinacea* functions better throughout the day. Finally, regardless of which cultivar of *P. australis* is selected, an appropriate density range of *P. australis* within the *P. arundinacea*–*P. australis* compound community is required to maintain the relative stability of the compound community according to the ability of *P. arundinacea* to effectively utilize weak light. Nevertheless, the difference in cultivars should be taken into account when the appropriate densities of *P. australis* are determined.

Acknowledgements

This work was financially supported by Project Supported by the National Natural Science Foundation of China (Grant No 31370448), Agricultural Science and Technology Independent Innovation Funds (Grant No CX(15)1004), Major Projects of Natural Science Research in Colleges and Universities, Jiangsu Province (15KJA2100001), and the Priority Academic Program Development of Jiangsu Higher Education Institutions (PAPD). We are grateful to anonymous reviewers for valuable comments and suggestions on the manuscript.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by the National Natural Science Foundation of China [grant number 31370448]; Jiangsu Agricultural Science and Technology Innovation Funds [grant number CX(15)1004]; Major Projects of Natural Science Research in Colleges and Universities, Jiangsu Province [grant number 15KJA2100001], and the Priority Academic Program Development of Jiangsu Higher Education Institutions (PAPD).

References

- Adams CR, Galatowitsch SM. 2005. *Phalaris arundinacea* (reed canary grass): rapid growth and growth pattern in conditions approximating newly restored wetlands. *Écoscience*. 12:569–573.
- Bains G, Kumar AS, Rudrappa T. 2009. Native plant and microbial contributions to a negative plant-plant interaction. *Plant Physiol*. 151:2145–2151.
- Březinová T, Vymazal J. 2014. Competition of *P. australis* and *P. arundinacea* in constructed wetlands with horizontal subsurface flow – does it affect BOD₅, COD and TSS removal? *Ecol Eng*. 73:53–57.
- Březinová T, Vymazal J. 2015. Evaluation of heavy metals seasonal accumulation in *P. arundinacea* in a constructed treatment wetland. *Ecol Eng* 79:94–99.
- Chen XS, Deng ZM, Xie YH, Feng L, Hou Z. 2014. Effects of sediment burial disturbance on the vegetative propagation of *Phalaris arundinacea* with different shoot statuses. *Aquat Ecol*. 48:409–416.
- Dushoff J. 2004. Comment on “Metapopulation persistence with age-dependent disturbance or succession”. *Science*. 304:684.
- Elonger A. 2009. Structure, growth dynamics and biomass of reed (*Phragmites australis*) - a review. *Flora*. 204:331–346.
- Fu WG, Li PP, Bian XM. 2007. Dynamics in the succession of vegetation communities in Inner-River wetland in Zhenjiang. *Resources and Environment in the Yangtze Basin*. 16:163–168.
- Fu WG, Li PP, Wu YY. 2011. Mechanism of the plant community succession process in the Zhenjiang Waterfront Wetland. *Plant Ecol*. 212:1339–1347.
- Fu WG, Wang FK, Yin QL, Ten BQ. 2015. Niche dynamics of species in succession process in the Wetland of Yangtze Rivers Lower Reach, China. *Plant Ecol Evol*. 148:43–51.
- Gagnon V, Maltais-Landry G, Puigagut J, Chazarenc F, Brisson J. 2010. Treatment of hydroponics wastewater using constructed wetlands in winter conditions. *Water Air Soil Pollut*. 212:483–490.
- Ge ZM, Zhou X, Kellomali S, Wang KY, Peltola H. 2011. Responses of leaf photosynthesis, pigments and chlorophyll fluorescence within canopy position in a boreal grass (*Phalaris arundinacea* L.) to elevated temperature and CO₂ under varying water regimes. *Photosynthetica*. 49:172–184.
- Hastings A. 2003. Metapopulation persistence with age-dependent disturbance or succession. *Science*. 301:1525–1526.
- Herr-Turoff A, Zedler JB. 2007. Does morphological plasticity of the *P. arundinacea* canopy increase invasiveness? *Plant Ecol* 193:265–277.
- Kercher SM, Herr-Turoff A, Zedler JB. 2007. Understanding invasion as a process: the case of *Phalaris arundinacea* in wet prairies. *Biol Invasions*. 9:657–665.
- Kulmatiski A, Beard KH, Meyerson LA, Gibson JR, Mock KE. 2011. Nonnative *Phragmites australis* invasion into Utah wetlands. *West N Am Naturalist*. 70:541–552.
- Lavergne S, Molofsky J. 2004. Reed canary grass (*P. arundinacea*) as a biological model in the study of plant invasions. *Crit Rev Plant Sci*. 23:415–429.
- Lavergne S, Molofsky J. 2006. Control strategies for the invasive reed canarygrass (*Phalaris arundinacea* L.) in North American wetlands: the need for an integrated management plan. *Nat Area J*. 26:208–214.
- Lou Y, Xue CQ, Liu FP. 2014. Vertical distribution of dominant families in forest communities based on forest inventory in Guangdong province. *J Cent South Univ Forest Technol*. 34:18–23.
- Martina JP, Ende CN. 2012. Highly plastic response in morphological and physiological traits to light, soil-N and moisture in the model invasive plant, *Phalaris arundinacea*. *Environ Exp Bot*. 82:43–53.
- Martina JP, Ende CN. 2013. Increased spatial dominance in high nitrogen, saturated soil due to clonal architecture plasticity of the invasive wetland plant, *Phalaris arundinacea*. *Plant Ecol*. 214:1443–1453.
- Martínková J, Klimešová J. 2017. Position of tillers in a clone determines their ontogeny: example of the clonal grass *Phalaris arundinacea*. *Folia Geobot*. 52:1–9.
- Nelson FM, Anderson ON. 2015. Variation among genotypes and source habitats in growth and fecundity of the wetland invasive plant *Phalaris arundinacea* L. *Wetlands*. 35:1175–1184.
- Pedescoll A, Sidrach-Cardona R, Hijosa-Valsejo M, Bécarea E. 2015. Design parameters affecting metals removal in horizontal constructed wetlands for domestic waste water treatment. *Ecol Eng*. 80:92–99.
- Perkins TE, Wilson MV. 2005. The impacts of *Phalaris arundinacea*, (reed canarygrass) invasion on wetland plant richness in the Oregon Coast Range, USA depend on beavers. *Biol Conserv*. 124:291–295.
- Perry LG, Galatowitsch SM. 2004. The influence of light availability on competition between *Phalaris arundinacea* and a native wetland sedge. *Plant Ecol*. 170:73–81.
- Perry LG, Galatowitsch SM. 2006. Light competition for invasive species control: A model of cover crop-weed competition and implications for *Phalaris arundinacea* control in sedge meadow wetlands. *Euphytica*. 48:121–134.
- Rodriguez M, Brisson J. 2015. Pollutant removal efficiency of native versus exotic common reed (*Phragmites australis*) in North American treatment wetlands. *Ecol Eng*. 74:364–370.
- Saltonstall K. 2002. Cryptic invasion by a non-native genotype of *Phragmites australis* into North America. *Proc Natl Acad Sci USA*. 99(4):2445–2449.
- Tucker CC. 1990. The genera of *Arundinoideae* (Gramineae) in the southeastern United States. *Arnold Arboretum*. 71:145–177.
- Uddin M, Caridi D, Robinson R. 2012. Phytotoxic evaluation of *Phragmites australis*: an investigation of aqueous extracts of different organs. *Mar Fresh Res*. 63:777–787.
- Vymazal J. 2011. Plants used in constructed wetlands with horizontal subsurface flow: a review. *Hydrobiologia*. 674:133–156.
- Vymazal J, Březinová T. 2016. Accumulation of heavy metals in above-ground biomass of *P. australis* in horizontal flow constructed wetlands for wastewater treatment: a review. *Chem Eng J*. 290:232–242.
- Vymazal J, Kröpfelová L. 2005. Growth of *P. australis* and *P. arundinacea* in constructed wetlands for wastewater treatment in the Czech Republic. *Ecol Eng*. 25:606–621.
- Wang YL, Cui XM, Lan L. 2015. Light and temperature and their effects on photosynthesis characteristics of stereoscopic cultivation in *Panax notoginseng*. *J Chinese Materia Medica*. 40:2921–2929.
- Xue CD, Feng JM, Wang XP. 2008. Vertical distribution patterns of plant species diversity in Northern Mt Gaoligong Yunna Province. *Chin J Ecol*. 27:323–327. [In Chinese].
- Zhang YL, Luo XM. 2008. Research progress of reed canary grass. *Acta Agrestia Sinica*. 16:661–666.