Differential effects of transgenerational plasticity on morphological and photosynthetic properties between an invasive plant and its congeneric native one

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Original Paper

Abstract Phenotype of plant offspring may be affected by particularly maternal environmental conditions, which is named as transgenerational plasticity. Transgenerational plasticity enhances the fitness of offspring under the maternal environmental conditions. Transgenerational plasticity may promote the successful invasion of alien plants, particularly those with clonal growth. However, few studies have compared transgenerational plasticity between alien invasive clonal plants and their congeneric native ones. A pot experiment with the invasive herb Wedelia trilobata and its congeneric native species Wedelia chinensis was conducted to investigate effects of light conditions (low vs. high light treatment) experienced by mother ramets on morphological and photosynthetic properties of offspring ramets subjected to the low light treatment. Compared with those of offspring ramets from mother ramets subjected to the high light treatment, leaf area, potential maximum net photosynthetic rate ($P_{\text{max}}$) and biomass accumulation of offspring ramets from mother ramets subjected to the low light treatment were significantly greater in W. trilobata than W. chinensis. Opposite pattern was observed in number of offspring ramets. We conclude that effects of transgenerational plasticity on growth performance could be species-specific between invasive plant and its congeneric native one. Positive effect of transgenerational plasticity on number of offspring ramets was not transformed into growth advantages of native species W. chinensis during its later establishment. However, favorable effects of transgenerational plasticity on capturing light resource could enhance competitive ability and promote successful invasion of W. trilobata.

Keywords Clonal plant · Morphological property · Photosynthetic property · Biomass accumulation · Invasion

Introduction

Clonal plants can propagate multiple ramets with identical genotype that remain connected to their parent ones at least during the early stage of development (Klimešová et al. 2016; Wang et al. 2020). Many of the world’s worst invasive plant species are clonal (Yu et al. 2009). In China, for instance, 67% of the most invasive plant species with extensive distribution or severe damage to local diversity are clonal plants (Liu et al. 2006; Wang et al. 2020). Thus, factors determining invasiveness of alien clonal plants has received increasing attention recently (Portela et al. 2020).

Phenotype of plant offspring may be affected by particularly maternal environmental conditions,
which is named as transgenerational plasticity (Galloway and Etterson 2007; González et al. 2016; Sobral et al. 2021). For example, germination rate of seed was significantly increased when *Campanula americana* was planted into its maternal light environment (Galloway 2005). Offspring of *Plantago lanceolata* subjected to their maternal nutrient treatment accumulated more biomass as well as greater storage of root carbohydrates (Latzel et al. 2014). Transgenerational plasticity allows offspring to form a ‘memory’ of the maternal environment, which enhances their fitness under the same environmental conditions (Ren et al. 2017; Dong et al. 2018).

Without meiosis during propagation process, effects of the environmental conditions experienced by mother ramets might be transmitted to their offspring ramets more stably and efficiently (Schwagerle et al. 2000; Douhovnikoff and Dodd 2015; González et al. 2016). Compared with offspring ramets from mother ramets subjected to the high light treatment, light capturing ability and utilization efficiency of offspring ramets from mother ramets subjected to the low light treatment were significantly improved (Li et al. 2018). Stolon internode length of offspring ramets subject to same foliar herbivory experienced by mother ramets was significantly increased in invasive plant *Alternanthera philoxeroides* (Dong et al. 2017). Compared with non-maternal light environment, biomass accumulation of offspring ramets subject to maternal light environment was significantly greater in the clonal invader (Dong et al. 2019). It is suggested that transgenerational plasticity may potentially contribute to successful invasion of clonal invaders (Dong et al. 2017, 2018, 2019; Portela et al. 2020).

A meta-analysis showed that phenotypic plasticity was significantly greater in invasive plants than non-invasive ones (Davidson et al. 2011). However, little effort has been dedicated to revealing the differential transgenerational effects between clonal invaders and their congeneric native species. Transgenerational plasticity can improve adaptation of their offspring to various environments when plants colonize into new habitat (Münzbergová and Hadincová 2017). So, it was hypothesized that invasive species exhibited greater transgenerational plasticity in morphological and photosynthetic properties than their congeneric native ones.

By using clonal invader *Wedelia trilobata* (L.) Hitchc and its congeneric native one *Wedelia chinensis* (Osbeck.) Merr, a pot experiment was conducted to test the hypothesis. Light is crucial for growth and development of *W. trilobata* and *W. chinensis* (Qi et al. 2014; Niu et al. 2019). In the experiment, mother ramets were grown under high or low light conditions respectively, whereas offspring ramets were subjected to the same low light conditions. We predicted that (1) effects of light treatment experienced by their mother ramets on morphological and photosynthetic properties (such as leaf area, stolon internode length and potential maximum net photosynthetic rate ($P_{\text{max}}$)) of offspring ramets were significantly greater in *W. trilobata* than *W. chinensis*; (2) effects of light treatment experienced by their mother ramets on number and biomass accumulation (such as leaf, stem, root and total biomass) of offspring ramets were significantly greater in *W. trilobata* than *W. chinensis*.

**Materials and methods**

**Plant species**

*W. trilobata* is a stoloniferous perennial herb originated from South America. As one of world’s worst invasive alien species, *W. trilobata* rapidly spreads and colonizes new habitats in Asia, North America, and Australia (Wang et al. 2017; Saptiningsih et al. 2018). In the late twentieth century, it was introduced to China as an ornamental plant. Now it is widely distributed in South China, such as Hainan, Jiangsu, Guangdong and Fujian provinces (Huang et al. 2022). As its congeneric native plant, stoloniferous perennial herb *W. chinensis* is generally distributed in woodlands, glades, forests edge and roadsides or creeks in southeast China (Hossen et al. 2020; Das et al. 2020).

Eight original plants of *W. chinensis* and *W. trilobata* were collected in Jiangsu, China (location 32°12’ N, 119°27’ E). Then, the original plants were propagated in a glasshouse with a natural day/night light cycle located at Sichuan Normal University, Chengdu, China (location 30°42’N; 102°84’E, altitude 540 m a.s.l). The glasshouse was maintained at a temperature of 20–28 °C and light intensity was equivalent to approx. 90% of full daylight outside the greenhouse. After 4 months, offspring ramets of each original plant formed a “ramet bank”.
Experimental design

*F₀ generation* F₀ generation of each species was subjected to two treatments (high light and low light) in the experiment. Two mother ramets with similar size (two leaves, 4 cm length roots) were chosen from “ramet bank”. Each ramet was grown in pot (32 cm × 37 cm × 24 cm) filled with substrate (3:1 mixture of humus soil and sand) respectively. Content of organic matter and total nitrogen was 66.3 g kg⁻¹ and 2.94 g kg⁻¹ in the substrate. Then, one ramet was subjected to high light treatment (full light), while the other was subjected to low light treatment (50% full light). Low light treatment was created by covering a neutral shading net (light transmittance is 50%). During the experiment, each pot was poured 100 mL Hogland nutrient solution with a concentration of 20% every week. Water was added to keep soil moist. All propagated ramets were named as F₀ generation in each pot.

*F₁ generation* One rooted ramet (two leaves, 4 cm length roots) subjected to high light or low light treatment was separated from F₀ generation of each species. Each separated rooted ramet was grown in pot (32 cm × 37 cm × 24 cm) filled with substrate (3:1 mixture of humus soil and sand). Then, each rooted ramet was subjected to low light treatment (50% full light). Low light treatment was created by covering a neutral shading net. During the experiment, 100 ml Hogland nutrient solution with a concentration of 20% was poured into each pot every week. Water was added to keep soil moist. All propagated ramets were named as F₁ generation in each pot (Fig. 1). Each treatment was replicated eight times. The whole experiment lasted 20 weeks.

Measurements

A fully expanded and mature leaf of offspring ramets (F₁ generation) was selected for photosynthetic measurement. Photosynthesis was measured using a portable photosynthesis system GFS-3000 (Heinz Walz GmbH, Effeltrich, Germany). Under a CO₂ pressure of 400 µmol mol⁻¹, PPFD was set from 0 to 1600 µmol mol⁻¹. Light–response curve [net photosynthesis rate (Pᵣ)–photosynthetic photon flux density (PPFD) curve] was generated according to the method proposed by Chen et al. (2015). \( P_{\text{max}} \) was calculated from \( P_{\text{net}} \)-PPFD curves fitted by a nonrectangular hyperbola model using the plotting software.

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![Schematic diagram of the experimental design](image-url)
Origin (Origin Lab, United States) (Gomes et al. 2006; Sorrell et al. 2012). Where Ø was the apparent quantum efficiency, θ was the convexity of the curve and \( R_d \) was the dark respiration rate.

After harvesting, stolon internode length and leaf area (WinFOLIA Pro 2004a, Regent Instruments, Inc., QC, Canada) of offspring ramets were measured. Then, offspring ramets were separated into leaf, stem (including petiole and stolon) and root, dried at 60 °C for 72 h and weighed. Leaf, stem and root biomass were calculated as well as total biomass.

Statistical analysis

Randomized block analysis of two-factor was used to investigate effects of block (original plant), maternal light condition (high/low light treatment) and species (invasive/native) on leaf area, stolon internode length, \( P_{\text{max}} \), total stolon length, number and biomass accumulation of offspring ramets (F1 generation).

All analyses were conducted with the R software (http://www.r-project.org/). Data calculation and statistical analysis were carried out by R package reshape (http://had.co.nz/) and R package agricolae (http://CRAN.R-project.org/package=agricolae).

Results

Leaf area of offspring ramets (F1 generation) was significantly affected by species, maternal light condition and their interaction (Table 1). Stolon internode length of offspring ramets (F1 generation) was significantly affected by species (Table 1). Compared with that of offspring ramets (F1 generation) from mother ramets subjected to the high light treatment, leaf area of offspring ramets from mother ramets subjected to the low light treatment was significantly greater in W. trilobata than W. chinensis (Fig. 2A). Significant effect of maternal light conditions on stolon internode length of offspring ramets (F1 generation) was not observed in the two species (Fig. 2B).

Potential maximum net photosynthetic rate (\( P_{\text{max}} \)) of offspring ramets (F1 generation) was significantly affected by species, maternal light condition and their interaction (Table 1). Compared with that of offspring ramets (F1 generation) from mother ramets subjected to the high light treatment, \( P_{\text{max}} \) of offspring ramets (F1 generation) from mother ramets subjected to the low light treatment was significantly greater in W. trilobata than W. chinensis (Fig. 3).

Number of offspring ramets (F1 generation was significantly affected by the interaction of species and maternal light condition (Table 2). Leaf, stem, root and total biomass of offspring ramets (F1 generation were significantly affected by species, maternal light condition and their interaction as well as total stolon length (Table 2). Compared with those of offspring ramets (F1 generation) from mother ramets subjected to the high light treatment, leaf area of offspring ramets from mother ramets subjected to the low light treatment was significantly greater in W. trilobata than W. chinensis (Fig. 3).

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| Effect | df | Leaf area | Stolon internode length | \( P_{\text{max}} \) |
|--------|----|-----------|-------------------------|------------------|
| B      | 7,21 | 1.47 ns   | 1.89 ns                 | 6.95* |
| S      | 1,21 | 14.98**   | 10.97**                 | 23.93*** |
| M      | 1,21 | 18.90**   | 0.15 ns                 | 17.27** |
| S×M    | 1,21 | 138.67*** | 0.01 ns                 | 21.14** |

Values give \( F \); symbols show \( P: \) *** \( P<0.001, \) ** \( P<0.01, \) * \( P<0.05, \) ns, non-significant, \( P>0.05 \)

**Fig. 2 Effects of transgenerational plasticity on morphological properties of offspring ramets (F1 generations). The colors in the columns represent different maternal light treatments. The same lower case letters are not significantly different at \( P=0.05 \). Values are means ± standard errors, \( n=8 \)**
Differential effects of transgenerational plasticity on morphological and photosynthetic properties of offspring ramets (F1 generation). 

Fig. 3 Effects of transgenerational plasticity on photosynthetic property of offspring ramets (F1 generation). The colors in the columns represent different maternal light treatments. The same lower case letters are not significantly different at $P = 0.05$. Values are means ± standard errors, $n = 8$.

to the high light treatment, number and total stolon length of offspring ramets from mother ramets subjected to the low light treatment was significantly greater in W. chinensis than W. trilobata (Fig. 4). Compared with those of offspring ramets (F1 generation) from mother ramets subjected to the high light treatment, leaf, stem, root and total biomass of offspring ramets from mother ramets subjected to the low light treatment was significantly greater in W. trilobata than W. chinensis (Fig. 5).

Discussion

Compared with that of offspring ramets from mother ramets subjected to the high light treatment, leaf area of offspring ramets from mother ramets subjected to the low light treatment was significantly greater in W. trilobata. Opposite pattern was observed in W. chinensis. Significant effect of maternal light treatments on stolon internode length of offspring ramets was not observed in the two species. Offspring ramets from mother ramets subjected to the high light treatment, $P_{\text{max}}$ of offspring ramets from mother ramets subjected to the low light treatment was significantly greater in clonal invader W. trilobata. Similar pattern was not observed in its native counterpart W. chinensis. The results supported our hypothesis.

Compared with those of offspring ramets from mother ramets subjected to the high light treatment, number of offspring ramets and total stolon length were significantly greater in W. chinensis. Without significant change of stolon internode length, total stolon length of W. chinensis significant increased with propagating more offspring ramets. Clonal plants often adopted morphological response such as stolon prolongation or petiole elongation to escape from low light condition (González et al. 2017; Li et al. 2018). Similar pattern was not observed in W. trilobata. So, we tentatively concluded that effects of transgenerational plasticity on growth performance of offspring ramets were species-specific between the two species. With greater $P_{\text{max}}$, invasive species allocated more nitrogen to its photosynthetic machinery than native species (Feng et al. 2007, 2008). A resistance-overcome strategy (bigger leaf and greater $P_{\text{max}}$) was employed by clonal invader W. trilobata and an avoidance strategy (longer total stolon length resulting from more ramets) was employed by its congeneric native one respectively (Galloway 2005; Marin et al. 2018). The possible explanation is that clonal invader W. trilobata may present greater threshold of shade tolerance in the experiment.

Positive association among leaf area, $P_{\text{max}}$ and biomass accumulation of offspring ramets was observed in W. trilobata. Similar effects of transgenerational plasticity was observed in stoloniferous herb Centella asiatica (Li et al. 2018). There was

| Table 2 ANOVA results for effects of block (B), species (S), maternal light condition (M) and their interaction on number of ramets, total stolon length and biomass accumulation of offspring ramets |
|-----------------|------|-----------------|------------------|------------------|------------------|------------------|------------------|------------------|
| Effect | df  | No. of ramets | Total stolon length | Leaf biomass | Stem biomass | Root biomass | Total biomass |
| B      | 7.21 | 1.68 ns       | 0.59 ns             | 1.09 ns      | 0.99 ns      | 1.11 ns      | 0.86 ns       |
| S      | 1.21 | 0.23 ns       | 35.67***            | 34.40***     | 35.96***     | 23.85***     | 89.35***      |
| M      | 1.21 | 4.80**        | 12.80**             | 29.63***     | 59.66***     | 28.83***     | 105.0***      |
| S×M    | 1.21 | 13.79**       | 40.61****           | 16.98**      | 34.73***     | 21.28**      | 63.03***      |

Values give $F$; symbols show $P$: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, ns, non-significant, $P > 0.05$
no significant effect on biomass accumulation of W. chinensis. A possible explanation is that higher resource capture ability and photosynthetic energy use efficiency of invasive plant may present positive associations with biomass accumulation (Shen et al. 2011; Funk 2013). The alternative explanation is that effects of transgenerational plasticity on propagation of offspring ramets may not transform into growth advantages of W. chinensis during its later establishment (Alba et al., 2011, 2016).

Transgenerational plasticity refers to the effect of maternal environment on offspring phenotype and phenotypic plasticity, which allows offspring to form a “memory” of maternal environment and helps them quickly adapt to environment (González et al. 2016; Fenesi et al. 2014; Portela et al. 2020). Favorable effects of transgenerational plasticity on leaf area, $P_{\text{max}}$ and biomass accumulation may be helpful for clonal invader W. trilobata to achieve larger final size and compete more intensely, which plays an important role in the successful invasion (Osunkoya et al. 2010; Geng et al. 2013; Zhang and Kleunen 2019).

Our experiment provides new insight into invasiveness of invasive plant with clonal growth, especially subjected to maternal environmental conditions. Evolutionary history of invasive species may be different from their congeneric native species. At the same time, transgenerational plasticity may be interfered by the evolutionary history of W. trilobata during invasion (Montesinos and Callaway 2018). It is suggested that a wider range of species pairs with overlapping distributions and similar evolutionary histories are used to investigate effects of transgenerational plasticity on growth performance and interspecific competitive ability between invasive plants and their congener native ones in the future.

![Fig. 4](image-url) Effects of transgenerational plasticity on number of ramets and total stolon length of offspring ramets (F$_1$ generation). The colors in the columns represent different maternal light treatments. The same lower case letters are not significantly different at $P=0.05$. Values are means ± standard errors, $n=8$. 
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Author contributions All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Xiao Xiao, Linxuan He, Xiaomei Zhang and Yu Jin. The first draft of the manuscript was written by Xiao Xiao. Jinsong Chen commented on previous versions of the manuscript and agreed to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved. All authors read and approved the final manuscript.

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Fig. 5 Effects of transgenerational plasticity on leaf, stem, root and total biomass of offspring ramets (F1 generation). The colors in the columns represent different maternal light treat-
ments. The same lower case letters are not significantly different at P=0.05. Values are means ± standard errors, n=8

Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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