

# The fitness optimization strategy under simulated warming An exploration on the reproductive pattern of the clonal submerged plant, *Potamogeton crispus* L.

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## Abstract

Reproduction determines the fitness and is a crucial component of life history. Asexual and sexual reproduction synergistically contribute to the fitness of clonal plants. Extreme warming leads to a periodical sharp rise in temperature and may affect the plant fitness. Few studies have concerned the impacts of extreme warming on the reproductive pattern of clonal aquatic plant and its evolutionary implication. In the present study, the cosmopolitan clonal submerged plant species, *Potamogeton crispus* L. from four different geographic sources, was subjected to simulated extreme warming. Both asexual and sexual reproductive performances including the recruitment of turions and fruits were evaluated. We found that both geographic source and warming significantly affected the reproductive performances. Although the response of turion number to warming was different for populations from different geographic sources, the turion mass did not decrease under warming. Moreover, warming induced a lower percentage of oligophyllous turions – the turion with no more than four scale leaves each, and a higher percentage of pleiophyllous turions – the turion with more than four scale leaves each. Additionally, warming caused a complete loss of sex for three populations. As the scale leaf functions as storage and photosynthetic organ and the scale leaf number is positively correlated with the axillary bud number, *P. crispus* may select to enhance the sprouting potential of turion to achieve the fitness optimization by enhancing the recruitment of scale leaves and thus larger turions under warming.

## 1 Introduction

As a crucial component of global environmental change, climate warming has been usually recognized as a graduated process (Seifert et al., 2015). However, in recent decades, an increase in the frequency and magnitude of climatic extremes has been obvious (Smith, 2011; Baldwin et al., 2019). Extreme weather event such as heat wave has swept the global and inflicted heavy losses on the human society (Sun et al., 2018; Baldwin et al., 2019). Meanwhile, extreme warming has been certified to impact the biosphere (Beznosov & Suzdaleva, 2004; Elias, 2018). The likelihood of extreme warming events has been predicted to increase and last longer, and the future scenario of climate warming may change (Sun et al., 2018).

As terrestrial ecosystem, aquatic ecosystem suffers the disturbance from climate warming as well (Beznosov & Suzdaleva, 2004; Audet et al., 2017). The effects of climate warming on the reproductive pattern of terrestrial plants have been equivocal – several studies have indicated a loss of sex and others reported the contrast (Dorken & Eckert, 2001; Pluess & Stöcklin, 2005; Klady et al., 2011; Dolezal et al., 2020). Shallow freshwater habitats are probably more sensitive to climate warming and their water temperature increases more rapidly than the temperature of deep water due to their close proximity to air (Mooij et al., 2008). Aquatic macrophytes are the major producers in the shallow freshwater habitats and prominently impacted by the climate warming (Beznosov & Suzdaleva, 2004). Climate warming has been proven to boost the growth

and expansion of several macrophyte species (Wu & Ding, 2019; Zhang et al., 2019). As a crucial stage of life history, the reproductive strategy of clonal macrophytes has been a key point for the understanding of their ecology and evolution (Franklin et al., 2021). However, the reproductive strategy of clonal macrophytes under climate warming has been understudied. Asexual clonal reproduction dominates in the breeding system of macrophytes especially for the submerged life-form. Hence, previous researches on the warming effects on the reproduction of macrophytes have mainly concerned clonal propagation. For instance, You et al. (2013, 2014) and Liu et al. (2016) found that warming promoted the clonal propagation of *Eichhornia crassipes*. Silveira & Thiébaud (2017) found that an increase in temperature favored the recruitment of lateral branches of *Elodea canadensis*. Yan et al. (2021) showed that warming enhanced the clonal asexual propagation of *Potamogeton crispus*. Prior researches have investigated the sexual reproduction of macrophytes in response to warming and showed that extreme warming impeded the sexual reproduction (Li et al., 2016; Xu et al., 2020; Yan et al., 2021). Most clonal plants possess two reproductive modes – they generate offspring sexually through seeds and asexually through vegetative propagules (Franklin et al., 2021). Sexual reproduction promotes the genetic differentiation of sexual offspring while asexual propagation enables the clonal progeny to conserve the genetic information from their genets (McKey et al., 2010). Therefore, the reproductive pattern – how the reproductive efforts are assigned in different reproductive modes, determines the fitness of clonal plants and have further evolutionary impacts (Wang et al., 2021b). The effects of clonality on sexual reproduction has been drawn increased attention in recent years (Barrett, 2015). The phenotypic plasticity in plant allocation has been verified to be prominent in response to climate change factor such as warming in a meta-analysis (Stotz et al., 2021). However, an integral exploration on the reproductive pattern of clonal aquatic macrophytes – how the reproductive effort is assigned under climate warming is scarce. Moreover, due to the clonal characteristic of most aquatic macrophytes, the potential difference in genetic background has been commonly neglected especially for the submerged plants despite that the geographic distance correlates with the genetic variance (Wu et al., 2015; Franklin et al., 2021). Despite the likely genetic variance among different clonal macrophyte populations, above studies on the reproduction of macrophytes merely considered plant materials from single geographic source and a broad perspective on the effects of geographic source on the reproductive pattern of macrophytes is scarce. Ecological and genetic factors may jointly contribute to the formation of reproductive pattern for clonal plants; however, the relative importance of environment and genetic background has been insufficiently evaluated (Eckert, 2002; Gillard et al., 2020).

*Potamogeton crispus* L. or the curly pondweed is a cosmopolitan clonal submerged plant species native to Eurasia (Jian et al., 2003; Heuschele & Gleason, 2014). Both asexual and sexual reproduction are available for this species (Xu et al., 2020; Yan et al., 2021). Hence, this species is an ideal model species for the study of reproductive pattern. Despite that, asexual propagation has been the major concern for the researchers since vegetative reproduction is the main reproductive mode (Heuschele & Gleason, 2014). The asexual propagule of *P. crispus* is called turion, which is a metamorphosis of shoot apices and a combination of modified, short leaves condensed on extremely shortened stems (Adamec, 2018). Turions or vegetative buds usually function as overwintering organs for many clonal macrophytes from temperate to polar regions (Adamec, 2018). However, the turion of *P. crispus* is dormant innately over the warm summer, germinates in winter or early spring, and the seeds and turions formed along with the decay of vegetative parts such as shoots in late spring or early summer (Sastroutomo, 1981; Heuschele & Gleason, 2014; Adamec, 2018; personal field observation). The formation of aestivated turions depends on the synergy of high temperature and long duration at high irradiance in early summer (Adamec, 2018). Therefore, climate warming can be expected to cause the transition of life history and alter the reproductive pattern of *P. crispus* (Xu et al., 2020; Yan et al., 2021). The morphology of turion has been a focus in several prior researches. For instance, Xie & Yu (2011) and Xie et al. (2015) found that the nutrient level determined the size and number of turion production. Qian et al. (2014) proved that water column phosphorus rather than water column nitrogen determined the number and biomass of turion production, and water nutrient level influenced the scale leaf number of turion and thus the turion size. Moreover, the metamorphosed leaves or the condensed scale leaves contain chlorophyll and can photosynthesize, which confer an ecological advantage on this species and help produce new organs (Adamec, 2018). Few studies concerned the sexual production of *P. crispus*. Xu et al. (2020) and Yan et al. (2021) reported that the sexual reproduction of *P. crispus* weakened under warming.

In the present study, four populations of *P. crispus* originated from different geographic sources were subjected to different situations of unwarmed and extreme warming (a 2–5.8 °C increase in water temperature) in a mesocosm experiment. The asexual propagation (turion production) and sexual reproduction (seed output) were evaluated to explore the reproductive pattern under warming. Following hypotheses were postulated:

1. Warming affects the production and morphology of asexual turions for *P. crispus* ;
2. A loss of sex exists under warming;
3. Fitness is optimized through alteration of reproductive pattern under warming.

## 2 Material and methods

### 2.1 Plant material

From June 20<sup>th</sup> to 30<sup>th</sup>, 2013, the turions were respectively collected from four distant populations of *P. crispus* in Gansu Province, which is located in the warm temperate zone of Northwestern China (Table 1). For each population, over 30 turions were carefully removed from the decaying shoots and placed into labeled plastic bags separately. After the collection, the turions were immediately delivered to the National Field Station of Liangzi Lake Ecosystem in the sub-tropical region of Central South China (30deg05'–30deg18' N, 114deg21'–114deg39' E) and separately stored in four 1000 ml beakers with 800 ml deionized water in the refrigerator at 0 °C. The deionized water of each beaker was replaced every three days. In December 15<sup>th</sup>, 2013, the turions from four distant populations were taken out of the refrigerator and respectively placed into 300 ml beakers with 250 ml of Liangzi Lake water. The beakers were placed on a table in the laboratory. The lake water was from an electric pump system linked to the Liangzi Lake. Each turion was placed into one beaker and the beakers were labeled to discriminate the geographic sources. The lake water of each beaker was replaced every three days. On January 21<sup>st</sup>, 2014, eight germinated turions with similar morphology and size (5–6 scale leaves, approximately 4 cm long for metamorphosed stem length and 3 cm wide for the distance between two largest opposite scale leaves, see the turion structure in Fig. 1) for each geographic source were selected for the mesocosm experiment.

### 2.2 Experimental set-up

The experiment was set up in the National Field Station of Liangzi Lake Ecosystem of Wuhan University, Hubei Province, China (N 30deg05'–30deg18', E 114deg21'–114deg39'). The mesocosm system was made up by 32 plastic tubs (60 cm in diameter and 65 cm in height). Each tub was filled with 15-cm-thick sediment collected from the bottom of Liangzi Lake. The lake sediment was sieved to remove aquatic plants and propagules, then mixed evenly before the experiment set-up. Then, Liangzi Lake water was carefully and fully added into each tub. The unwarmed treatment or the control (CK) was established by placing 16 mesocosms in an outdoor platform (10 m L x 10 m W). A 3-meter-high transparent rainproof roof was set up above unwarmed mesocosms to prevent disturbance from rainfall (Wang et al., 2021a). The warming treatment was mimicked by placing the remaining 16 mesocosms in a glasshouse (Liu et al., 2016; Yan et al., 2021). Four selected germinated turions were respectively planted into the center of the sediment of four unwarmed and warming mesocosms. Thus, each treatment of geographic source and warming was replicated four times. The experiment started on January 22<sup>nd</sup>, 2014. During the experiment, each mesocosm was checked every three days. The algae and snails on the plant body were carefully removed to prevent the disturbance to the growth of *P. crispus* from these organisms. Each mesocosm was also confirmed to be full-filled with lake water by adding lake water throughout the experimental period. The day water temperature of each mesocosm was measured every five days using the YSI Professional Plus water quality probe (YSI Co, OH, USA) at 8:00, 12:00 and 18:00. The mean water temperature in the glasshouse was 2–5.8 °C higher than that outdoor (Fig. 2).

### 2.3 Harvest and measurement

The plant materials were harvested on May 7<sup>th</sup>, 2014 after 106 days of growth when the plant vegetative parts entered the decaying process. First, the fruit sets were collected. Second, all turions in each mesocosm

were collected. The number of fruits and turions were counted. The scale leaf number of each turion was recorded. Then, the biomass of fruits and turions was determined after oven-drying at 70 °C for 48 h. Since the scale leaf number of turion ranged from 1 to 8 in the present experiment, the turions were divided into two groups based on the scale leaf number – the oligophyllous turion (the turion with scale leaf number  $\leq 4$ ) and the pleiophyllous turion (the turion with scale leaf number  $> 4$ ). This classification method for turion has been certified to be effective in discriminating its fitness since scale leaf number has a direct correlation with the turion sprouting potential (Jian et al., 2003; Qian et al., 2014). The percentage for each group was calculated.

## 2.4 Statistical analysis

All data met the assumption of normality and homogeneity. Two-way ANOVA was performed to test the effects of geographic source and warming condition on the reproductive traits. Independent sampled t test was performed to check the difference between different warming conditions for each plant from different geographic sources. All data analyses were performed using SPSS 22.0 (SPSS, Chicago, Illinois, USA).

## 3 Results

Warming condition, geographic source, and their interactions had significant effects on all measured traits including turion number, turion biomass, percentage of oligophyllous turions, percentage of pleiophyllous turions, fruit number and fruit biomass (Table 2).

### 3.1 Asexual reproduction

Warming significantly decreased the turion number for Population 1 and increased the turion number for Population 2 (Fig. 3A). No significant variation in turion number was shown between different warming conditions for the other populations (Fig. 3A). Warming significantly increased the turion mass for Population 2 and no significant variation in turion mass was shown for the remaining populations (Fig. 3B). Warming significantly decreased the percentage of oligophyllous turions and increased the percentage of pleiophyllous turions for all populations (Fig. 3C & D).

### 3.2 Sexual reproduction

Warming decreased the sexual reproduction of three populations to zero while the sexual reproduction of Population 4 was constantly zero under different warming conditions (Fig. 4A & B).

## 4 Discussion

### 4.1 Warming shifted the metamorphosis for turion formation

The warming effects on the reproductive quantity of vegetative propagules were complex, since a decreased turion number for population 1, an increased turion number for population 2 and a consistency in turion number for population 3 and 4 were observed under warming. However, considering turion biomass, despite an increased turion biomass was shown for population 2 under warming, the remaining three populations displayed a coherence in turion biomass production under warming. Namely, the turion biomass production did not decrease under warming. In terms of turion biomass production, at least *P. crispus* could maintain its fitness under warming. Extreme warming was observed to advance the initial time for turion formation in the present study. However, the turion biomass production was unresponsive to warming. The decay rate of macrophyte shoots has been positively correlated with temperature (Li et al., 2021). Extreme warming may boost the decay of plant shoots, which may disturb the formation of turions since turions are innately the metamorphosis of apical shoots (Adamec, 2018). *P. crispus* has been widely considered to be tolerable to environmental stresses such as eutrophication and heavy metal pollution (Cao et al., 2009; Qiao et al., 2015). From the perspective of asexual reproduction, the strong tolerance capacity of *P. crispus* appeared to be certified once again. However, the present result for turion production has certain discrepancy with a recent report from Yan et al. (2021), which showed an increasing turion production under warming. The turions used for the experimental set-up in our experiment originated from four distant populations in the warm temperate zone while the material source of Yan et al. (2021)'s study was populations in Liangzi Lake

from sub-tropical region. The linear distance between the sampling site of Yan et al. (2021)'s study and that of Population 1 in our study is over 1300 km. Local adaptation and differentiation of plant ecotypes may occur among these populations since geographic distance is relevant with genetic variance (Wu et al., 2015; Franklin et al., 2021). Thus, the plant populations from warm temperate region are speculated to be less sensitive in clonal reproduction to warming than that from subtropical zone. The underlying mechanism for the difference in clonal reproduction among different climate zones has not been explored for clonal macrophytes and needs further investigation.

Intriguingly, *P. crispus* decreased the production of oligophyllous turions and produced more pleiophyllous turions under warming. Considering the modular structure of turion, this strategy may contribute to the enhancement of fitness for *P. crispus*. First, pleiophyllous turions are larger in size than oligophyllous turions. Larger vegetative propagules with more scale leaves likely have larger nutrient reserve and thus possess greater longevity and vitality (Xie & Yu, 2011). Second, the scale leaves possess the photosynthetic potential. Pleiophyllous turions may take the advantage of higher photosynthetic efficiency and thus help produce new organs more rapidly (Adamec, 2018). Lastly, a pleophyllous turion has more axillary buds than an oligophyllous turion. The axillary buds are the sole modules for the generation of young seedlings. Therefore, pleiophyllous turions probably have greater germination potential than oligophyllous turions (Qian et al., 2014). Overall, the production of more pleiophyllous turions is likely a strategy of fitness optimization for *P. crispus* under warming.

#### 4.2 A complete loss of sex under extreme warming

Despite that clonal plants usually retain two reproductive modes – sexual seed reproduction and asexual vegetative propagation, a loss of sex has been widely recognized in the evolutionary process of clonal plants (Eckert, 2002). Two prior studies have found that warming reduced the sexual reproduction of *P. crispus* in the measurement of inflorescence number (Xu et al., 2020; Yan et al., 2021). Although inflorescence can indicate sexual reproduction, fruits or seeds are more directly correlated with plant fitness (Wang et al., 2021b). In the present study, we found a rare complete loss of sex under extreme warming as warming blocked the production of fruit sets for three populations, which corresponds to the second hypothesis. During the experimental process, inflorescence has also been observed. However, no fruit sets formed in the warming treatments. The major pollination mode for *P. crispus* is hydrophilous (Guo & Huang, 1999). High water temperature likely damaged the pollen viability, which led to the failure in the seed formation (Rang et al., 2011). Santamaria & Hootsmans (1998) also found that the seed production of the submerged plant, *Ruppia drepanensis* was blocked when the water temperature exceeds 30 . Therefore, a probable explanation for the complete loss of sex is that extreme warming disrupted the pollen viability.

#### 4.3 Fitness optimization - an integral view of reproductive pattern

Reproductive pattern – how reproductive effort is allocated in different reproductive modes is directly correlated with the fitness of clonal plants (Wang et al., 2021b). The shift in reproductive pattern in different ecological conditions, as a representative of adaptive phenotypic plasticity, likely optimize the fitness of clonal plants in changing scenarios (Li et al., 2018).

In an integral view, the tested four populations from different geographic sources showed an adaptive plasticity in reproduction pattern under different warming conditions. First, population 1 and 3 showed a maintenance in asexual propagation especially the turion biomass production under different warming conditions, while the sexual reproduction was totally lost under warming. This shift in reproduction pattern seems a non-adaptive plastic response to warming. However, it is noteworthy that a higher percentage of pleiophyllous turions generated under warming. Since the scale leaf is correlated with the nutrient storage, photosynthetic capacity and the axillary bud number thus the sprouting potential, an increase in the percentage of pleiophyllous turions likely enhances the fitness and thus compensates the complete loss of sex (Xie & Yu, 2011; Qian et al., 2014; Adamec, 2018). Second, population 2 presented an increase in clonal propagation and simultaneously a decrease in sexual reproduction under warming. A prominent trade-off between asexual and sexual reproductive modes was shown in the shift of reproductive pattern (Herben et

al., 2015). Although warming blocked the sexual reproduction and thus impeded the probable genetic variance in the progeny, the enhancement in the asexual propagule production is likely beneficial in maintaining the fitness. Lastly, population 4 also showed a coherent asexual propagation output under varied warming conditions. However, warming did not alter its sexual reproduction as no sex reproduction was manifested under both unwarmed and warmed conditions. As population 1 and 3, more pleiophyllous turions were recruited for population 4 under warming, and the fitness maximization might be realized. Overall, the fitness of the populations from four different geographic sources is predicted to be optimized under extreme warming.

## 5 Conclusion

In the present study, warming exerted mixed effects on the reproductive pattern of the four populations from different geographic sources. First, the variation in turion number output was complex among different populations and the turion biomass production maintained or increased under warming. Second, warming induced a metamorphosis shift in turions, as a lower percentage of oligophyllous turions and a higher percentage of pleiophyllous turions generated. Lastly, a complete loss of sexual reproduction existed under warming. Generally, *P. crispus* showed an optimization in reproductive strategy through the adaptive phenotypic plasticity in reproductive pattern when facing warming scenario. The geographic distance likely induces local adaptation and the formation of different ecotypes of *P. crispus*. Since this mesocosm experiment used asexual propagules from warm temperate region of China, future studies should consider different propagule types and a larger scale of geographic sources for these propagules. Furthermore, a transplant experiment cross different climate zones may provide a global perspective in the reproductive strategy of clonal macrophytes and thus a deeper understanding in its evolutionary implications.

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## Data Accessibility Statement

The data that support the findings of this study are openly available in Dryad.

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**Table 1 The geographic source of the turions**

	Longitude (E)	Latitude (N)	Site	Habitat type
Population 1	103.1542556°	36.9493622°	Tianzhu County	River
Population 2	102.1069033°	38.2034026°	Yongchang County	River
Population 3	99.8972554°	39.3003924°	Gaotai County	Pond
Population 4	96.3710793°	40.5687570°	Guazhou County	Reservoir

**Table 2 F-values and significances of two-way ANOVA of the effects of warming condition and geographic source on reproductive performance**

	Warming condition (W)		Geographic source
	F	P	F
<b>Turion number</b>	8.028	0.009	17.513
<b>Turion biomass</b>	16.400	<0.001	15.674
<b>Percentage of oligophyllous turions</b>	116.139	<0.001	19.325
<b>Percentage of pleiophyllous turions</b>	116.139	<0.001	19.325
<b>Fruit number</b>	4517.296	<0.001	1688.423
<b>Fruit biomass</b>	1024.135	<0.001	285.713

Fig. 1 Picture of turion structure. The turion of *P. crispus* is a vegetative propagule with a propeller shape. The metamorphosed stem and metamorphosed leaf/scale leaf are the modules of condensed apical shoots. An axillary bud generates on the metamorphosed stem between two scale leaves. Young seedlings sprout from the axillary buds

Fig. 2 Mean daytime water temperature throughout the experimental period. The mean daytime water temperature was approximately 2–5.8 higher under warming condition than under normal condition

Fig. 3 Variation in (A) turion number, (B) turion biomass, (C) percentage of oligophyllous turions and (D) percentage of pleiophyllous turions under different warming conditions for the four populations from different geographic sources

Fig. 4 Variation in (A) fruit number and (B) fruit biomass under different warming conditions for the four populations from different geographic sources





