



Asymmetric pollen–pistil interactions contribute to maintaining floral colour polymorphism in a clonal aquatic plant (*Butomus umbellatus* L.)

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ABSTRACT

Floral colour polymorphism occurs in many species throughout the angiosperms but the mechanisms of selection remain unclear. In this study, we studied the pollen–pistil interactions between different *Butomus umbellatus* plants, a clonal aquatic plant with red and white-flowered individuals. Results indicated that red-flowered plants have lower asexual and sexual reproductive output compared to white-flowered plants in monomorphic populations, even though there are no differences in flower characteristics and pollination systems. On the other hand, in polymorphic populations, sexual reproductive output in red-flowered plants increases while asexual reproductive output decreases considerably. However, this remains unaffected in white-flowered plants. Artificial pollination treatments revealed asymmetric pollen–pistil interactions between red and white-flowered individuals. Inter-morph crosses increase seed production only when the red-flowered plant is maternal. Moreover, pollen grains of white-flowered plants significantly enhance not only female fitness by way of greater seed yields, but also male fitness by promoting fertility of pollen on stigma within a flower. Such special pollen–pistil interactions might form one kind of balancing selection and actively maintain both genotypes of the two morphs. These findings may enrich our understanding of mechanisms of maintaining plant reproductive polymorphism.

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1. Introduction

Floral colour polymorphism occurs in many species throughout the angiosperms (Levin and Kerster, 1970; Schemske and Bierzychudek, 2001; Pannell et al., 2005). There is a debate over the roles and mechanisms of natural selection in floral colour polymorphisms (Schemske and Bierzychudek, 2001), which seemingly vary among plant species and among populations within a species (Schemske and Bierzychudek, 2001; Jersakova et al., 2006). In general, pollinator preferences (Gigord et al., 2001), fluctuating selection due to temporally varying environments such as precipitation (Schemske and Bierzychudek, 2001) have been cited as the possible mechanisms of selection. Studies of floral colour polymorphism mainly focus on the reproductive fitness of each morph and the mechanisms of maintenance of different morph frequencies (Levin and Brack, 1995; Gigord et al., 2001; Schemske and Bierzychudek, 2001; Jersakova et al., 2006). Actually, reproductive interactions due to inter-morph pollination in polymorphic populations may occur frequently because pollinator preference is not

as widespread as expected for plants with floral colour polymorphisms (Levin and Brack, 1995; Schemske and Bierzychudek, 2001; Jersakova et al., 2006). Since pollen performance in a given pistil may be affected by the pollen genotype (Herrero and Hormaza, 1996), inter-morph pollen–pistil interactions may have different reproductive performances compared to pollination within each morph. Such kinds of pollen–pistil interactions may provide new insights into the mechanism of floral colour polymorphisms.

Flowering rush (*Butomus umbellatus* L., Butomaceae) is a clonal aquatic monocot that inhabits shallow waters around the margins of lakes, slow-flowing rivers, and a variety of wetlands from northern Asia, Europe and North America (Sun, 1992; Hroudova et al., 1996). An individual plant consists of a monopodial rhizome that bears basal leaves and inflorescences. Generally, an umbel-like inflorescence consists of 15–50 flowers (Sun, 1992). Each flower has three sepals, three slightly larger petals, nine stamens and six apocarpous carpels (Sun, 1992). Typically, flowers of the plants have red gynoecia (R morph). A new morph of flowers with white gynoecia (W morph) was recently found in northeastern China (Huang and Tang, 2008). Fluctuating selection by water levels is regarded as one possible mechanism causing the colour polymorphism (Tang and Huang, 2010). However, the patterns and consequences of pollen–pistil interactions between red and white-flowered plants remain unclear. We hypothesize

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that inter-morph rather than intra-morph pollination enhances sexual reproductive performance. To test the hypothesis, we first investigated the reproductive performance of flowering rush in the monomorphic and polymorphic populations. Additionally, asexual and sexual investment, flower characteristics and pollination of red and white-flowered plants from both the monomorphic and polymorphic populations were compared to detect any differences affecting reproductive output. We then conducted artificial pollination treatments at both inter and intra-morph levels to reveal the potential differences. Based on the findings we discuss the mechanisms of maintaining floral colour polymorphism in the species.

2. Materials and methods

2.1. Study species and site

B. umbellatus plants display both asexual and sexual reproduction. In the case of asexual reproduction, plants produce clonal bulbils not only on rhizomes, but also at the base of inflorescences (Eckert et al., 2000). Inflorescence bulbils develop near the end of the flowering period, and remain attached to the inflorescence until it decomposes. Sexual reproduction of the species exclusively depends on pollinators, which are attracted by nectar secreted from nectaries located at the bottom of the carpels (Bhardwaj and Eckert, 2001). The species is dichogamous and fully self-compatible; outcrossing is promoted through strict protandry (Eckert et al., 2000). Seed production in *B. umbellatus* is low but highly variable (Krahulcova and Jarolimova, 1993; Fernando, 1996; Fernando and Cass, 1997a). The considerable prevalence of development irregularities in both the male and female reproductive components of the species is largely responsible for the low levels of sexual reproductive success as opposed to environmental factors (Fernando and Cass, 1997a,b).

Field investigations and artificial pollination treatments were conducted in Hexiangyuan wild lotus garden in Mishan county (45.51 N, 131.86 E), Heilongjiang Province of China. Monomorphic populations of both red and white-flowered individuals (R and W morph), as well as polymorphic populations were present in the site. Three lakeside populations, including two monomorphic populations (one R morph and one W morph) and one polymorphic population were used in this study. Before hand pollination, at least 50 individual plants representing both R and W morphs were enclosed with fine bridal veil netting before the flowers opened in order to exclude pollinators.

2.2. Differences in reproductive performance of plants in monomorphic and polymorphic populations

To test the hypothesis that plants of R and W morph exhibit different reproductive performance between the monomorphic and polymorphic populations, seed production per fruit and offspring survival ability were investigated in 2006 and 2007. At least 100 capsules from 100 individual plants were randomly picked for seed count. Offspring survival ability was estimated by seed mass (mg) and germination rate, which was carried out by using a group of 100 individual seeds. For germination rate, the seed samples were placed on filter papers in Petri dishes and kept in a growth chamber at a temperature and light regime of 14 h light/25 °C and 10 h dark/10 °C. The number of germinated seeds was determined daily until no more seeds germinated (for c.4 weeks). Percentage germination rate was expressed as the total number of germinated seeds. At least 30 and 10 batches were used to estimate seed mass and germination rate, respectively.

To detect any factors affecting the potential differences in reproductive output between plants of R and W morph in both the

monomorphic and polymorphic populations, asexual and sexual investment, flower characteristics, as well as pollination, were compared in 2006 and 2007. Leaves per plant and bulbils per inflorescence were used to evaluate asexual investment. Except for seeds per fruits, inflorescences per plant and flowers per umbel were also investigated to reveal sexual investment. For the investigation on asexual and sexual investment, at least 50 individual plants were randomly selected. When studying flower characteristics, flower longevity, pollen viability and pollen and ovule production were examined. Thirty flowers were randomly selected from different inflorescences to estimate the longevity of a single flower. Floral longevity (hours) was noted by recording the length of time it took for petals in a single flower to unfold and wither. To count pollen and ovule number per flower, 20 mature flowers from different individuals were randomly picked during the blooming period before anther dehiscence. The method followed Yang and Guo (2004). Pollen grains collected from 30 individual plants were stained with 2, 5-diphenyl tetrazolium bromide (MTT) to reveal pollen viability. The methods followed Li et al. (2012).

Pollination observations were conducted at peak blooming periods. The total time taken in each type of population was more than 120 h; from 10:00 to 12:00 and from 14:00 to 16:00 on fine weather days. Pollinator type, pollination frequency and efficiency, and pollinator behaviour were compared between plants of R and W morph from both the monomorphic and polymorphic populations. Pollinators were captured immediately after visiting a flower for later identification. Pollination frequency is roughly equal to the number of visits made to a single umbel by all kinds of pollinators within an hour (the number of individual flies h⁻¹ per umbel). Five randomly selected umbels were used during the peak blooming period to calculate average pollination frequency in each population. The number of visited flowers within an umbel during a single foraging trip by a single insect was also noted to reveal any possible change in pollinator behaviour. Pollination efficiency was estimated by stigmatic pollen load, which were collected from 50 pollinated flowers. To count pollen grains deposited on stigma, six carpels of each flower were carefully separated from the flowers and observed under a fluorescence microscope (Nikon E-600) after treatment with 8 mol L⁻¹ NaOH for 24 h, followed by 0.1% aniline blue dye. Pollen load was determined at the level of an individual flower.

2.3. Pollen–pistil interactions

To reveal the patterns of pollen–pistil interactions between plants of R and W morph, intra and inter-morph hand pollination were conducted in 2007. For intra-morph pollination, selfing (S, pollen grains from the same flower), geitonogamous (G, pollen grains from the same umbel) and outcrossing pollination (pollen grains from other individuals; hereafter, R and W refer to outcrossing pollen grains of R and W morph, respectively) were randomly applied to flowers of the same morph. For inter-morph hand pollination, pure pollen grains of R morph were deposited on stigma of flowers of W morph and vice versa. For each treatment, at least 30 flowers were hand-pollinated and left to set fruit. Seed production per fruit was used to detect any differences in pollen–pistil interactions between plants of R and W morph.

It is generally difficult to distinguish seeds with different paternal sources when pistils bear mixed stigmatic pollen loads. Therefore, we designed an experiment whereby hand pollination was used to detect how pistils with pure stigmatic pollen loads (intra- or inter-morph pollen grains) affected reproductive outputs of neighbouring pistils (hand pollination simulating natural conditions) within a single flower for the two morphs (“neighbouring effect” experiment) in 2007 and 2008. Where pollinators displayed no discrimination between flowers of R and W morphs during a

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