The dynamics of island populations of *Platanthera bifolia* in the Biebrza National Park (NE Poland)

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Two isolated populations of *Platanthera bifolia* (Orchidaceae) were monitored for six years in the Biebrza National Park. *Platanthera bifolia* populations seem to be affected by habitat conditions. The populations differed in size, proportion of flowering individuals and the effectiveness of reproduction. The natural fruiting rate of *P. bifolia* is high (over 90%), due to high levels of autogamy (almost 60%). Some costs of reproduction (in terms of reduction of leaf size) were observed. Leaves were largest before flowering and in subsequent years their size decreased. Dormancy affected population dynamics, varying from 22.4% in one population to 16.3% in the other. Both *P. bifolia* populations appeared to be healthy and are not threatened with extinction at the two study sites.

Key words: autogamy, cost of reproduction, dormancy, flowering, fruiting, orchids, *Platanthera bifolia*, population dynamics

Introduction

Information on biology and demography of orchid species is still limited given the size of the Orchidaceae, reaching 20 000 species (Atwood 1986). Orchidaceae is one of most interesting plant families because of a large variation of life history strategies. Among members of this family are short- and long-lived species, clonal and non-clonal species, and a wide range of pollination mechanisms (Tremblay 1992). Generally, however, there has been a trend toward decreasing numbers of orchid species on all continents, mainly due to human activity. Therefore, the necessity of monitoring of changes in orchid populations has been recently stressed by many authors, because according to Ackerman (1998) "populations are the basic unit of species conservation". In most cases monitoring of orchid populations follows year-to-year changes in numbers of individuals, their flowering and fruiting rates, the frequency of dormancy and the costs of reproduction (Wells & Willems 1991, Waite *et al.* 1991). Such studies, however, usually do not report important information on mortality and reproduction rates — ecological processes shaping population dynamics. Specificity of orchid life histories, for example long time of below-ground growth or phenomenon of dormancy, makes analyses of dynamics of orchid populations difficult.

This paper is one of the reports on the dynamics of island populations of orchid species



Fig. 1. Localities of the *Platanthera bifolia* populations and the distribution of individuals in the year of their maximum abundance, 1999.

in the Biebrza National Park, Poland (Brzosko 2002a, 2002b). Here, I present the results of multi-year observations of two *Platanthera bifolia* populations. The objective of this project was to describe the dynamics of the two populations studied, and to examine some aspects of biology of this species with respect to habitat conditions.

Bog orchids, *Platanthera*, are found in moist habitats in temperate and subtropical regions (Patt *et al.* 1989). *Platanthera bifolia* is a common terrestrial orchid in Poland, where it occurs in a variety of forest and meadow habitats. The species is a polycarpic perennial. Typically, it has two ovoid leaves at the base of a single flowering stem. The inflorescence spike displays white flowers. The flowers producing nectar and attracting noctuid long-tongued moths (Sphingidae, Noctuidae) have a strong, sweet scent (Nilsson 1992). Flowers open sequentially, and after two-three weeks all the flowers are open. Only a few flowers in the lower part of the spike may wither before that. A mature capsule contains up to 8000 seeds (Maad 2000).

Material and methods

Platanthera bifolia populations were studied in the Biebrza National Park, NE Poland. The Zabudnik population (ZAB) was located on a typical island dune, with ridges or fused parabolic forms, within a mosaic of widespread peat bogs (Żurek 1975). The dune covers a subpeaty surface and the soils are fluvial of eolian and river origin. The island is about 1.2 m above the surrounding peat and its total area is 5500 m². A very small percentage of the island supports an oak-linden-hornbeam forest. The remaining parts are covered by small individuals of Betula pubescens, Rhamnus cathartica and Viburnum opulus. Calamagrostis epigejos forms large patches. The second population (FORT) is situated on the periphery of an old fortification from the First World War, about twelve kilometres from the ZAB population. Vegetation around the fortification is dominated by pine (Pinus sylvestris) forest. A P. bifolia population was found on the banks of a water-filled moat. The soil moisture was higher in that location than in the neighbouring pine forest, because the orchid site was adjacent to the moat. Vegetation cover was sparser than in the pine forest; from 10% to about 50% of the soil was covered by herbs, with the following dominating: Fragaria vesca, Melampyrum pratense, Leontodon hispidus, Convallaria majalis, Anthriscus sylvestris and Maianthemum bifolia. Populus tremula dominated the tree layer and leaves of this species covered the soil at the study site.

FORT population covered about 100 m². Some of the individuals were found among the concrete debris of old fortifications.

Observations were carried out over six years (1996-2001) in the ZAB population and during five years (1997-2001) in the FORT population. Plants were individually marked and mapped (Fig. 1). This allowed to monitor individual plants in subsequent years, as well as to detect and analyse the phenomenon of dormancy (the absence of above-ground shoots). Those analyses included only individual plants with above-ground shoots present in the first and in the last year of monitoring. Each year the observations were carried out in late June, when the flowers were fully open. Fruiting took place in July and August. For each plant the following parameters were recorded: (1) reproductive status: flowering, non-flowering, (2) length and width of the largest leaf, (3) height of flowering stem and the length of inflorescence; and (4) three measures of reproductive success were applied: number of flowers per plant,



Fig. 2. Numbers of *Platanthera bifolia* individuals in the Biebrza National Park (lines) and proportion of flowering individuals (bars). Total population is the sum of above-ground plants.

number of fruits per plant and percent of fruit-set. Each year (in June and July) the study sites were searched for new plants. In 2001 a pollination experiment was carried out. Five inflorescences were covered by cotton net in the ZAB population to evaluate seed production without pollinators (autogamy). These inflorescences were covered before any flowers were open and the cotton net remained in place until fruiting time.

The influence of light on flowering and fruiting was evaluated using 1998 and 1999 data for the ZAB population. This was tested in the ZAB population only because almost all individuals in the FORT population grew in shade. Reproducing plants growing in full light were compared with flowering plants in the shade for the length of inflorescence, number of flowers and fruits per flowering stalk. The cost of reproduction was calculated as the reduction of leaf size in years following flowering.

Results

Population size

Individuals of *Platanthera bifolia* grew in aggregations of different sizes at both sites (Fig. 1). The number of plants in the FORT population (Fig. 2) varied from 205 (2000) to 292 (1999). In the ZAB population the number of individuals, except 1996 and 1997, when only a fragment of population was observed, ranged from 352 (1998) to 458 (2000) (Fig. 2). The average density of plants in year of maximum abundance varied from 0.6/10 m² in the ZAB population to 19.4/10 m² in the FORT population. 3

Successive years of flowering

4

5



2



Fig. 4. The number of years between flowering events for individuals of *Platanthera bifolia*.



Fig. 5. The mean size (± 1 standard error) of flowering and non-flowering individuals of *Platanthera bifolia* in the two populations studied.

Flowering

Among the one hundred individuals in the ZAB population that were present in 1996, twenty-five never flowered. Thirty individuals flowered once, and the number of individuals that flowered two

or three times was twenty. A few individuals flowered four or five times (Fig. 3). In the FORT population the frequency of flowering was lower and almost half of them (49.3%) never flowered. The proportion of individuals that flowered once or twice was 33.5% and 19.3%, respectively.

Frequency (%)

0

0

1



Fig. 6. Annual mean number of flowers and fruits per flowering individual (± 1 standard error) in the two *Platanthera bifolia* populations.

Seven individuals (3.3%) in the FORT population flowered three times, and only one flowered four times (Fig. 3). The proportion of flowering individuals varied considerably from year to year, especially in the ZAB population, where from 21.8% to 64.5% flowering plants was observed (Fig. 2). In the FORT population the proportion of flowering individuals was lower and ranged from 2.7% to 28.3% (Fig. 2). The lowest proportion of flowering plants in both populations was in 2001 (the next year after drought).

Some of the inflorescences were damaged by frost, drought or grazing by animals. The losses of inflorescences ranged from 4.4% to 33.7% of in the ZAB population and from 14.3% to 31% in the FORT population. The largest number of damaged inflorescences (31.5% in ZAB and 31% in FORT) was noted in the driest year, 2000. In the year 2001, 33.7% of inflorescences of the ZAB population were lost due to frost. Flowers on damaged inflorescences did not produce pollen. The majority of the plants flowering two or more times flowered in consecutive years or with a one-year interval (Fig. 4).

Size of inflorescences

The average length of inflorescences ranged from 10.0 ± 2.9 cm to 13.0 ± 3.8 cm in the ZAB population and from 5.6 ± 2.5 cm to 13.3 ± 3.2 cm in the FORT population (Fig. 5d). Significant differences between years were found (F = 7.595 and 38.158; df = 530 and 157; respectively; p < 500

0.001). The inflorescences were shortest in both populations in 2000 (the year of drought) and longest in 1999 (Fig. 5d). Two populations differed in this parameter in 1998 and in 2000 (F = 12.254 and 74.641; df = 248 and 119; p < 0.001).

Number of flowers

The average number of flowers per inflorescence over the observation period varied from 12.8 ± 4.1 in 1997 to 17.5 ± 3.5 in 2001 in the ZAB population and from 13.1 ± 4.2 in 2000 to 17.8 ± 5.4 in 1999 in the FORT population (Fig. 6). There were significant differences between years (ZAB/FORT: F = 8.003/5.460; df = 526/153; p < 0.01) and between populations in 1997 (F = 9.112; df = 56; p < 0.01) and 1999 (F = 5.333; df = 133; p < 0.05). There was a significant positive correlation between inflorescence length and the number of flowers per inflorescence; r = 0.77 for the FORT population, and r = 0.63 for the ZAB population, p < 0.05.

The total number of flowers ranged from 105 to 908 in the FORT and from 410 to 3386 in the ZAB population.

Fruiting

Most of the undamaged flowering plants formed fruits. In the FORT population, in four out of five years fruits were observed on 100% of the flowering individuals. In 2000 (year of the drought),



Fig. 7. Fruit-set in the two *Platanthera bifolia* populations.

the proportion of fruiting plants was 82.5%. In the ZAB population from 62.3% (2001) to 100% (1997) of the plants formed fruits.

In both populations fruit set and mean number of fruits per plant were lowest in 2000 (Figs. 6, 7). The mean number of fruits per spike varied from 7.2 ± 5.3 to 14.2 ± 6.0 in the ZAB (F = 30.627; df = 513; p < 0.001) and from 4.4 ± 4.0 to 14.8 ± 7.0 in the FORT population (F = 20.714; df = 152; p < 0.001) (Fig. 6). The populations differed significantly with respect to these traits in three out of five years (F = 10.692 - 17.106; df = 63-113; p < 0.01). The total number of fruits produced in the ZAB population ranged from 328 (1997) to 2735 (1998) and in the FORT population from 41 (2001) to 555 (1998). Thus, the number of seeds ranged from 2 624 000 to 21 880 000 in the ZAB, and from 328 000 to 4 440 000 in the FORT population. The number of fruits per inflorescence was positively correlated with the number of flowers per inflorescence (r = 0.76 in ZAB and r = 0.72in FORT) and with the length of inflorescence (r = 0.62 in ZAB and r = 0.72 in FORT).

Overall, fruit set was high in both populations and ranged from 47% to 91.3% in ZAB and from 33.7% to 84.2% in FORT (Fig. 7). Four out of the five inflorescences covered with nets produced fruits. Among the 103 flowers present on those inflorescences 60 (58.3%) set fruits.

Effect of light on flowering and fruiting

In the ZAB population, where the effect of light on flowering and fruiting was evaluated, plants growing in full light had longer inflorescences and produced more flowers and fruits. Inflorescence length in shaded places reached 11.0 \pm 4.7 cm in 1998 and 1999, while in full light averaged 11.9 \pm 3.1 cm and 13.6 \pm 3.7 cm in successive years. The numbers of flowers per plant were 16.5 \pm 4.5 and 13.4 \pm 6.5 in the shade, and 18.7 \pm 6.1 and 15.6 \pm 4.5 in sunny places in 1998 and 1999, respectively. The numbers of fruits produced by plants growing in the light did not differ significantly between the consecutive years and averaged 15.3 \pm 5.0 and 14.6 \pm 4.4, respectively. Likewise, the numbers of fruits produced by plants growing in the shade also did not differ and averaged 13.5 \pm 6.8 and 12.1 \pm 6.2, respectively.

Size of plants

The height of flowering plants in the ZAB population significantly varied between 1997 (42.5 ± 14.4 cm) and 1998 (48.6 ± 8.2 cm, F = 7.305; df = 551; p < 0.001, Fig. 5a). Also in the FORT population the mean height differed statistically significantly between 1997 (50.1 ± 9.7 cm) and 2000 (27.2 ± 8.2 cm, F = 54.486; df = 170, p < 0.001, Fig. 5a). The two populations differed in the height of flowering plants in 1997, 1998 and 2000 (F = 5.968/79.258; df = 68/250; p < 0.05).

Flowering plants had larger leaves than nonflowering ones (Fig. 5b, c, e and f). In the ZAB population in 1996 the length and width of the leaves averaged 15.2 ± 2.6 cm and 4.3 ± 1.1 cm, respectively, whereas in 2000 they averaged 16.1 \pm 3.8 cm and 3.8 \pm 1.1 cm, respectively (Fig. 5b and c). The leaves of flowering plants in the FORT population were, on average, 13.7 ± 1.9 cm long in 2000 and 16.6 ± 2.3 cm long in 1999. Their width ranged from 3.5 ± 0.9 cm in 2000 to 4.8 ± 1.1 cm in 2001 (Fig. 5b and c). There were no significant between-year differences in leaf size of flowering plants in the ZAB population, but in the FORT population the length and width of leaves differed in consecutive years (F= 8.789; df = 185; and F = 6.915; df = 185; p <0.001, respectively). Between-population differences in the length of leaves of flowering plants were significant only in 2000 (F = 19.113; df = 151; p < 0.001).



Fig. 8. Percentage of individuals that remained dormant for different times at both sites. The percentages only include the individuals that were present at the first and at the last year of the monitoring period.



Non-flowering plants had smaller leaves than flowering plants (Fig. 5). In the ZAB population the mean leaf length differed significantly between the two years of study (F = 4.347; df = 1019, p < 0.001) and averaged 12.8 ± 3.5 cm in 1997 and 11.1 ± 4.2 cm in 2001. Likewise, in the FORT population the mean leaf length differed significantly between the year 1997 (13.0 \pm 3.9 cm) and 2000 (10.0 \pm 2.8 cm, F = 17.133; df = 908, p < 0.001, Fig. 5e). In the ZAB population the mean width of leaves of non-flowering plants was 3.1 ± 1.2 cm in 1997 and 2.3 ± 1.2 cm in 2000 and differed statistically between the years (F = 7.795; df = 1020; p < 0.001). Also in the FORT population the difference between mean leaf width in 2000 (2.1 ± 0.9 cm) and 2001 ($2.8 \pm$ 1.4) was statistically significant (F = 8.065; df = 907; p < 0.001, Fig. 5f). The two populations differed in the leaf length of non-flowering plants in the two last years of study (F = 34.215/12.844;



Fig. 9. Proportion of dormant individuals of *Platanthera bifolia* in the two populations studied.

df = 460/422; p < 0.001). Between-population differences in the width of leaves were significant in the first and last year of study (F = 6.002/5.940; df = 276/421; p < 0.05).

Dormancy

All individuals of Platanthera bifolia did not produce aerial shoots every year. Ninety-eight individuals at the ZAB site and 49 at the FORT population were observed in the first and the last year of study. Between 33.7% and 42.9% of the individuals were dormant at least once in the populations studied. Most often the period of dormancy lasted one year (Fig. 8). In the ZAB population 24.5% and in the FORT population 29.6% of the individuals were dormant once during the study. A two years' dormancy was only observed in 4.1% of the individuals in the FORT population and in 8.2% in the ZAB population. Dormancy longer than two years was only observed in the ZAB population (Fig. 8). Five plants (10.2%) in this population were absent above-ground for three or four years. The effect of dormancy on the population dynamics differed between years (Fig. 9). The percent of individuals which were absent above-ground ranged from 12.2% (1998) to 22.4% (2000) in the ZAB population, and from 1% (1998) to 16.3% (1999 and 2000) in the FORT population (Fig. 9). A significant difference between the frequency of dormancy of flowering and non-flowering plants was noted. During the study period non-flowering individuals entered dormancy more often (on average 17.7% of the individuals in the FORT and 19% in the ZAB population) than flower-



Fig. 10. The leaf size (length and width) of *Platanthera bifolia* individuals before and after flowering. 0 = year of flowering. Values are means and ± 1 standard error.

ing ones (14.8% and 8.2% of the individuals in the respective populations). The probability of flowering decreased after dormancy. Most of the flowering plants (80% in the FORT, and 69.2% in the ZAB population) were non-flowering after dormancy.

Costs of reproduction

In the ZAB population leaf size increased significantly in the years before flowering, then decreased during two consecutive years after flowering and levelled off for the next two years (Fig. 10). In the FORT population leaf size achieved a maximum when the plants were flowering (Fig. 10). In the first and second year after flowering the length and width of the leaves decreased, and then, in the third year, increased.

There were no significant changes in shoot height, leaf size, inflorescence length or the number of flowers and fruits among the plants that flowered in two or more consecutive years. In both populations values of these parameters varied slightly in consecutive years of flowering.

Discussion

The development of *Platanthera bifolia* populations seemed to be influenced by habitat conditions. The total number of plants in the small area of the FORT population was only about 50% lower than the number of plants in the larger area occupied by the ZAB population. Possibly, the environmental conditions in the surroundings of old fortification (mainly the larger area of bare soil due to lower cover of other plant species) were more suitable for the appearance of new individuals (higher number of younger individuals appeared here than in the ZAB population, where the soil is densely covered by plants). The same results were previously obtained for Cypripedium calceolus populations (Brzosko & Werpachowski 1998, Kull 1998, Brzosko 2002a), for Listera ovata (Brzosko 2002b), and for Liparis loeselii (Jones 1998) where the proportion of seedlings in a population was strongly affected by the area of bare soil and litter cover. Orchids have been recorded in new, synanthropic habitats (Adamowski 1998, Cohn et al. 2001). Adamowski (1998) noted that orchids can colonise anthropogenic habitats. He also reported almost a 40-fold increase in numbers of P. bifolia population during the seven-year study carried out in a poplar plantation. Old fortifications were probably such a new habitat for P. bifolia. Also soil moisture seemed to be an important factor affecting population dynamics of P. bifolia. In the ZAB population, where moisture of soil was variable in different parts of the island, P. bifolia was only present in wetter parts. Individuals of the FORT population were not observed in higher and dryer areas.

The frequency of flowering and the proportion of flowering individuals were greater in the ZAB than in the FORT population. Perhaps the light conditions were more favourable for flowering in the ZAB population, where many places were well-lit, whereas the plants of the FORT population grew only under a canopy of trees and shrubs. Plants growing in full light had longer inflorescences and produced more flowers and fruits than those growing in shade, although the differences were not significant. In some orchid species light conditions affect flowering and fruiting as much as weather conditions (Case 1987, Firmage & Cole 1988, Mehroff 1989, Farrell 1991, Wells & Cox 1991, Willems & Bik 1991, Wells *et al.* 1998, Maad 2000). It seems that other factors, such as drought and frost influenced flowering and fruiting in the *P. bifolia* populations. In 2000, an exceptionally dry year, the length of inflorescences as well as the number of flowers and fruits per plant were lowest, and the individual plants were smallest, especially in the FORT population. On the other hand, the proportion of flowering plants was lowest in the year after drought, when exceptional spells of frost occurred in May.

Another factor determining the reproductive output of Platanthera bifolia populations seems to be the condition of a plant, expressed in size. Plant size determines the onset of flowering in other orchid species (Calvo 1990, Wells and Cox 1991, Whigham & O'Neill 1991, Willems & Bik 1991, Wells et al. 1998, Willems & Dorland 2000). For example, Wells et al. (1998) found that the probability of flowering increases with an increasing leaf number. Flowering individuals of P. bifolia had larger leaves than non-flowering ones, and the leaf size increased significantly before flowering. Individuals of P. bifolia which flowered once were smaller than those flowering two or more times. It therefore seems that only more vigorous plants can flower in consecutive years.

Individuals of Polish and Scandinavian populations of *P. bifolia* are similar with respect to many traits, but the Polish plants are higher than Swedish ones (Maad 2000) and they produce higher numbers of flowers and fruits than Finnish ones (Mattila & Kuitunen 2000). I also found greater between-year differences in the above parameters as compared with Maad's (2000) results.

High level of autogamy (almost 60%) may explain high fruit set (exceeding 80%–90%) in the studied populations. Autogamy renders *Platanthera bifolia* almost independent of pollinators. High fruiting rates were also noted by Maad (2000) in Swedish populations. Schmidt and Antlfinger (1992) noted that reproduction in *Spiranthes cernua* was predominantly agamospermous. This mating system allows colonising small, isolated habitats and sustains small populations. Those authors pointed out that low numbers of pollinators probably contributed to high levels of agamospermy. The pollinator limitation hypothesis suggests that the observed fruit production is below some optimal level that would otherwise be achieved if pollinators were more abundant (Calvo & Horvitz 1990). If this holds, then hand-pollinated flowers should have a significantly higher probability of setting fruit than naturally pollinated ones (Gregg 1989, Waite et al. 1991, Whigham & O'Neill 1991, Willems & Lahtinen 1997, Neiland and Wilcock 1998). Some authors suggest that capsule set in Platanthera species is pollinator-limited. In P. stricta (Patt et al. 1989), P. blepheriglottis (Cole & Firmage 1984), P. chlorantha (Nilsson 1978), P. ciliaris (Robertson & Wyatt 1990a, 1990b) and Finnish P. bifolia (Mattila & Kuitunen 2000) experimental hand pollination yielded fruit set levels higher than those observed in naturally pollinated orchids.

Flowering and fruiting in a given year affect future growth and reproduction of terrestrial orchids (Snow & Whigham 1989, Primack & Hall 1990, Primack & Stacy 1998), because the resources used up in the present reproduction are not available for the future reproductive events (Primack & Hall 1990). The size and reproductive success of a plant may depend on its ability to store resources before flowering (Calvo 1990). My results clearly showed that flowering in a given year resulted in a decrease of P. bifolia leaf size in consecutive years. This negative effect of flowering on future leaf size was only observed in individuals flowering once, and I did not notice any costs of reproduction in the individuals flowering in two or more consecutive years. The flower stalks of P. bifolia did not display a decrease in parameters observed during consecutive years of flowering. Individuals that flowered more than once were the most vigorous, because their leaves were greater than those of the plants flowering once. In subsequent years reproductive costs in Cypripedium acaule were clearly manifested as the reduction of probability of flowering and of plant size (Primack & Hall 1990, Primack & Stacy 1998), and the same applies to Listera ovata (Brzosko 2002b), as well as to some other orchid species (Whigham & O'Neill 1991, Calvo 1993). However, in Finnish populations of P.

bifolia (Mattila & Kuitunen 2000) no immediate costs of reproduction were noted, since the rate of capsule production in consecutive years did not affect the probability of flowering.

Orchids are characterized by an ability to enter dormancy (Lesica & Steele 1994, Hutchings et al. 1998, Willems & Melser 1998, Shefferson et al. 2001) and its prevalence is site-specific (Shefferson et al. 2001). Dormancy period was shorter in Platanthera bifolia than in other orchids studied in the Biebrza National Park (Cypripedium calceolus and Listera ovata; Brzosko 2002a, 2002b) or in species studied by other authors (Hutchings 1987, Mehroff 1989, Calvo 1990, Gregg 1991). Nevertheless, unlike in L. ovata (Brzosko 2002b), dormancy was very important for the population dynamics of P. bifolia, because nonflowering individuals entered dormancy more often than flowering ones. The probability of flowering decreased after dormancy in P. bifolia, similarly to Isotria medeoloides (Mehroff 1989). On the other hand, a return from dormancy to flowering condition was observed in Cyclopogon cranichoides (Calvo 1990), Cleistes divaricata (Gregg 1991) and Cypripedium candidum (Falb & Leopold 1993). The ability to enter dormancy may increase survival of the plant under unfavourable conditions in a growing season (Wells 1967) and may enhance restoration of resources (Willems & Dorland 2000).

Platanthera bifolia populations in the Biebrza National Park, as island-type populations, totally depend on the local ecological processes. The production of seeds and recruitment are clearly adequate to maintain or even increase the population sizes. Thus, P. bifolia populations in this area are not threatened with extinction from natural causes in the nearest future. On the other hand, high levels of autogamy and small population sizes are on the negative side (Whigham & O'Neill 1991). Defragmented and spatially isolated populations may be exposed to reduced gene flow and loss of allelic variation (Frankel & Soule 1981, Frankel et al. 1995, Gustafsson 2000). Small populations are also subject to genetic drift and inbreeding, which promote genetic erosion. Genetic analyses are needed to test whether the genetic variability in P. bifolia populations is reduced due to small population size and high level of autogamy.

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