Pollination Ecology and Reproductive Potential of *Jankaea heldreichii* (Gesneriaceae); a Tertiary Relict on Mt Olympus, Greece

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ABSTRACT

Jankaea heldreichii, a monotypic species of the Gloxinia family and a Tertiary relict, is restricted only to Mt Olympus (Greece). Its phenology of flowering, breeding system, mode of pollination, and reproductive potential were studied. Results showed that, although confined to a small area, this important plant species is not at present seriously endangered. Its vulnerability depends mostly on tourist pressure and uncontrolled collection.

INTRODUCTION

Greece is endowed with many endemic taxa—739 according to IUCN Threatened Plants Committee Secretariat (1982) and 1220 according to Iatrou (1986). One of these is *Jankaea heldreichii* (Boiss.) Boiss., a Tertiary relict and one of the five surviving European members of an otherwise tropical (and subtropical) family, the Gesneriaceae, which consists of about 1100 species. Three of the European species occur all over the Balkan Peninsula, one only in the Pyrenees and the fifth, *Jankaea heldreichii*, is restricted to Mt Olympus—the highest mountain in Greece (2917 m)—where over 1500 species of seed plants have been recorded. This floral richness is related to its long geographical isolation, to the unusual range of climatic conditions, where a high mountain is situated close to the sea, and the meeting of Mediterranean and Central European floras. Its major importance,

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however, lies in it being a major refuge of ancient European species (Polunin, 1980).

J. heldreichii, this 'living fossil', occurs in damp, shaded crevices of limestone rocks near permanent or semi-permanent streams in the beech forest zone, between *c.* 700 and 1400 m, mainly on the east and north sides of the mountain. It has been recorded, however, as low as 400 m and as high as 2400 m; it is most abundant between 600 and 800 m (Strid, 1980 and pers. comm.). It is included by the IUCN Threatened Plants Committee Secretariat (1982) among the 'vulnerable' taxa.

There is no information as to the mode of pollination of such relict species. Some data are available on the tropical and subtropical members of the family: it is noted that some bear nectaries (Fahn, 1979*a*; Opler, 1983), and there is evidence of chiropterophily (Vogel, 1958).

The absence of any data on the reproductive potential of such an important species led us to undertake this work. Its mode of pollination and reproductive capacity (seed setting, germination success) were studied in an attempt to examine the vulnerability of the species and to find clues for its restricted distribution.

Botanical characters

J. heldreichii is an acaulescent perennial herb with a basal leaf rosette. The scapes, usually single, appear from the centre of the rosette, 3–10 cm long, bearing 1–3 nodding flowers. The calyx is divided into 5 lobes, *c.* 3·5 mm long; the corolla is broadly campanulate, 11–16 mm long, pale lilac to bluish lilac, divided to the middle into 4 (rarely 5) obovate lobes. It holds 4(5) stamens with short filaments in the corolla tube; the anthers, as long as the filaments (*c.* 2·5 mm), are ovoid and rather bluish; style, *c.* 7 mm long, narrowly clavate; ovary superior, 1-locular; capsule ovoid, acute, *c.* 7 mm long, with numerous very small seeds (Rix & Webb, 1972; Strid, 1980).

METHODS

Study area

Preliminary observations on habitat preference and measurements of population sizes of *J. heldreichii* were made on Mt Olympus. Two study sites were chosen at 1160 and 1340 m (N and NE exposure) on the basis of accessibility and population sizes, allowing for an adequate number of observations and measurements. Both of these sites belong to the mixed zone of beech–fir–black pine forest.

The study period lasted from May to August for two consecutive years (1986–87).

Flowering records

J. heldreichii flowers from mid-May to mid-August according to altitude (Strid, 1980). A number of flowering buds (15) were marked on 1 July 1987 at the 1340 m site (peak of flowering) to give information on the phenology and duration of the flowering process. Observations were made on a daily basis.

Breeding system and seed setting

In order to determine whether *J. heldreichii* possesses the character of spontaneous autogamy, 112 flowering buds were covered with pieces of fine gauze to prevent access by pollinators. Another 16 flowers were cross-pollinated by hand. To this aim buds of these flowers were emasculated and dehisced anthers of nearby flowers were passed repeatedly over their stigma with a thin pair of forceps. After that, they were enclosed in fine pieces of gauze to avoid free pollination. Artificial cross-pollination was repeated every two days until the end of anthesis.

The number of capsules formed under both treatments was measured. In parallel, all individual flowers (277) having passed through the flowering stage in one locality were counted, and of these the number bearing fruits. The number of seeds produced was counted in 12 of these capsules.

Pollinators and floral rewards

Observations and capture of pollinators took place from 0700 h to sunset for a total of 15 days distributed throughout the flowering period of *J. heldreichii*. The insects collected were identified to species level. In a few cases the pollen loads carried were weighed and microscopically examined (Hodges, 1974).

Tests were made in order to check for the presence of nectar, (i) by the use of Drummond 10 μl micropipettes; (ii) by anatomical observations of the flower to detect presence of nectaries (Wallace, 1977; Fahn, 1979*a,b*); and (iii) by a chemical test with H_2SO_4 (95–97%) and 5% phenol solution (Clark, 1964; Schemske *et al.*, 1978).

Germination

Seeds collected from both free-pollinated and artificially cross-pollinated plants were tested for germination success. Fifty seeds from each treatment

(two replicates) were put into Petri dishes, on a sheet of filter paper, with 8 ml of deionized water. They were left to germinate in the dark at $15 \pm 2°C$. Records on the germination process were made on a weekly basis.

RESULTS

J. heldreichii is encountered only in damp and shady crevices of limestone rocks. Characteristically, it grows on the north and rarely on the eastern sides of these rocks. Its density varies: 25–50 rosettes m^{-2} are often encountered but there are also extremes of 100 rosettes m^{-2}, as well as the sporadic appearance of individual plants.

In the study sites, flowering started in late May and lasted about two months. The mean duration time of anthesis for each flower was 10 days (range 6–13). Blossoms are unscented, brightly coloured, purplish blue to purple, according to the 1976 CIE UCS Chromaticity Diagram (Keller, 1983). Flowers are homogamous (as defined by Percival, 1969).

Table 1 gives the results of the experiment with plants covered by fine pieces of gauze. Absence of any fruit setting provides good evidence that there was no spontaneous autogamy. Comparing the results from free pollination and artificial cross-pollination (Table 1), it can be seen that the success in fruit setting was relatively higher in the case of free pollination. Nevertheless, a firm statement cannot be made, taking into account the different sizes of the two samples.

The number of minuscule seeds included in each capsule is very high. In medium sized capsules, 235 seeds were counted (SE = 15·2, n = 6); in large capsules 613 (SE = 14·7, n = 3), whereas in small capsules there were 134 (SE = 6·9, n = 3).

Table 1 also shows the fairly low percentage of flowers surviving to reach the fruiting stage (< 50%). Predation and natural elimination, possibly due to hard climatic conditions, might be the factors responsible.

Germination experiments with seeds produced after free and artificial cross-pollination showed a high germination success (Fig. 1), but more pronounced in the case of free-pollinated flowers (83% versus 62%). In parallel, there was a remarkable delay in germination in the case of artificially cross-pollinated flowers.

J. heldreichii has a prominent entomophilous syndrome; it has a bright corolla colour, its anthers are hidden deep in the corolla tube and its stigmatic surface is not freely exposed. Changes in flower characteristics through time that might influence the pollination mode, as occurs, for example, in *Cyclamen repandum* (Kugler, 1977) and *C. graecum* (unpublished data), were not observed. Additionally, this plant occurs in the understorey

TABLE 1

Survival and Fruit-set of *Jankaea heldreichii* Flowers under Three Pollination Treatments: Covered Plants, Artificially Cross-pollinated and Free-pollinated

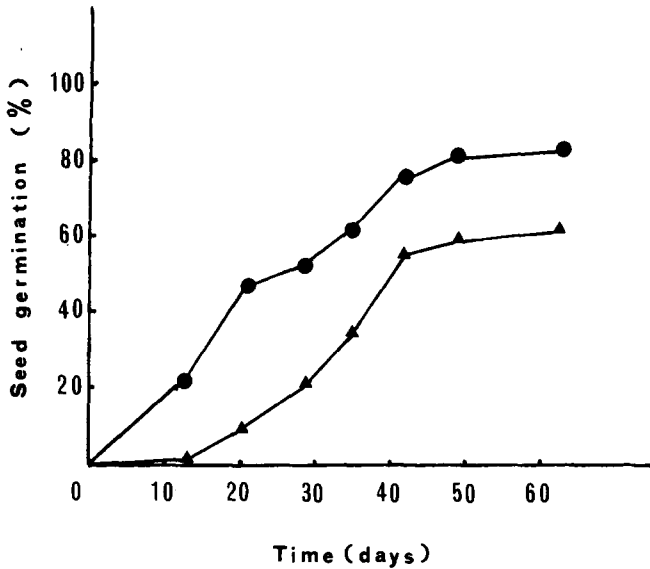|	Altitude (m)	Date of covering	No. of flowers tagged	Date of observations	No. of flowers recovered	No. of flowers setting fruit	% survival	% success in fruit-setting
Covered plants (test for autogamy)	1 160	12 June 1987	83	26 June 1987	41	0	49·4	0
	1 340	2 July 1987	29	9 August 1987	10	0	34·5	0
Artificially cross-pollinated	1 340	3 July 1987	16	18 August 1987	8	5	50·0	62·5
Free-pollinated	1 340	—	—	18 August 1987	277	189	—	68·2

Fig. 1. Germination process of *Jankaea heldreichii* seeds, resulting from free pollination (●) and artificial cross-pollination (▲).

or in sheltered sites, where its flowers have almost the same orientation. Both these factors do not favour wind pollination.

Apart from its floral and habitat characteristics which suggest insect pollination, the fact that none of the covered flowers produced any seed at all (Table 1) indicates that *J. heldreichii* is a strictly entomophilous plant (the fine gauze used excluded insects but not pollen grains).

Throughout the period of study, only 37 pollinators were recorded visiting the plants and 12 of these were captured. All were bumblebees, the species identified being *Bombus lucorum* (L.), *Pyrobombus soroeensis proteus* (Gerst.) and *P. pratorum* (L.). Therefore, pollinator visits could be characterized as scarce. It is noteworthy that 9 out of the 12 bumblebees captured were queens (three *B. lucorum*, three *P. soroeensis* and three *P. pratorum*), the rest being workers of *B. lucorum*.

Bumblebee activity started early in the morning, the first visit being recorded at 0750 h and the last at 1450 h. The peak of activity was between 0800 and 1100 h. In general, every visit lasted about 4–7 s but it was not unusual for a bumblebee to leave the flower after 1 s. The maximum time recorded was 15 s. On most occasions, the bumblebee moved successively to many adjacent flowers, penetrating the flower tubes to the upper part of its thorax.

Tests in the field with micropipettes for the presence of nectar proved negative and the same holds for both microscopic observations of the floral

anatomy and chemical tests. It seems that this relict plant has not evolved nectaries like some other tropical members of the same family (Fahn, 1979*a*; Opler, 1983). However, the foraging behaviour of bumblebees is similar to that of insects penetrating the flower to reach the nectar at the bottom, and could be explained in terms of feasibility of pollen collection from stamens located deep in the flower tube. All captured bumblebees carried pollen loads of considerable size—14 mg in the three cases weighed. Microscopic analysis of the pollen loads revealed presence of pollen from plant species other than *Jankaea*. However, in all cases the proportion of *Jankaea* pollen grains was significantly higher.

DISCUSSION

J. heldreichii is an insect-pollinated plant, but no particular relationship between it and its insect partners seems to have evolved. Taking into account the scarce visits of these pollinators to *J. heldreichii*, and the population sizes of both the plant and its pollinators, it could be argued that the nutritional requirements of these insects could not be satisfied by this plant alone. Nectar, an indispensable element of bumblebees' diet and absent in *J. heldreichii*, is offered by other plant species, and particularly by *Geranium macrorrhizum* L., a very well-represented species occurring in almost all the range of *Jankaea* on Mt Olympus. It is noteworthy that all three pollinators of *J. heldreichii* were also captured while visiting *G. macrorrhizum*, and the frequency of their visits was far higher.

Another point of interest is that the blossoms of *J. heldreichii* closely resemble in both colour and size, those of many *Campanula* spp., which are well distributed on Mt Olympus. Additionally, their major areas of occurrence (ravines) are the same. Some of the main pollinators of Campanulae are bumblebees. It could be argued, therefore, that this similarity might lead to visual attraction of their pollinators to *Jankaea*, with beneficial results.

The low frequency of pollinator visits to *J. heldreichii* flowers implies that this plant is not particularly preferred by its pollinators. Nevertheless, the plant relies on them for its survival. This may explain the prolonged duration of anthesis of each flower and, in spite of the limitations of the pollination process, it seems that the whole mechanism is quite efficient.

We cannot give any clear-cut explanation as for the preponderance of queens among pollinators captured. It is known, however, that after hibernation queens forage, particularly for pollen, which is made into clumps for egg-laying.

This rare endemic plant is not at present endangered, its population size

being adequate to secure survival of the species. The fact that it utilizes at least three different species of insects may be considered advantageous, since it may overcome unpredictable changes in pollinator availability. In spite of the relatively high natural mortality, its success in fruit setting is quite high. Additionally, it produces an extremely large number of minuscule seeds, which germinated readily. Its 'vulnerable' status is therefore not due to physiological constraints. The risks derive from increased human presence in the area for tourism, and especially from intense and uncontrolled plant collecting even though its area of occurrence is within the Mt Olympus National Park.

On the basis of the above data, it could be argued that the reasons for its confinement to Mt Olympus are related to its specific habitat preference for limestone crevices. However, *Jankaea* cannot be considered as an alpine species since it is encountered as low as 400 m. It seems that conditions prevailing at lower altitudes make this plant less competitive in comparison to others. Therefore, lowland Olympus acts as a barrier, impeding further expansion of this plant, in the same way as island endemic species are restricted.

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