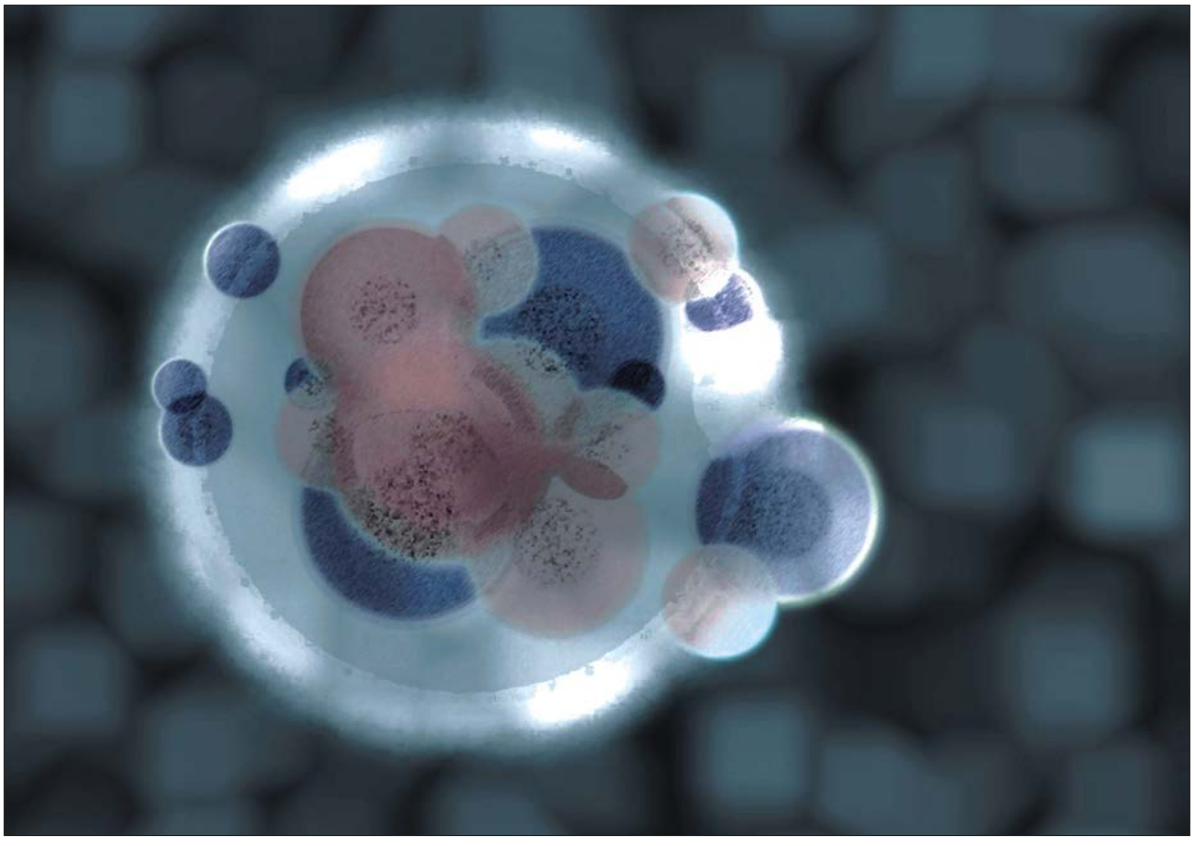

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Reproductive Ecology of an Endemic Angiosperm, *Meconopsis latifolia* Prain (Papaveraceae), in the Kashmir Himalaya, India

[1]A.R. Dar, [2]Zafar Reshi and [2]G.H. Dar
[1]Department of Botany, Government Degree College (Khanabal) Anantnag, Jammu and Kashmir, India
[2]Department of Botany, University of Kashmir, Srinagar-190 006, Jammu and Kashmir, India

Abstract: Seven spatially separate populations were studied in an attempt to identify and understand the bottlenecks that are responsible for the restricted occurrence and limited size of the existing populations of an endemic species, *Meconopsis latifolia*, in the Kashmir Himalaya, which is at the brink of extinction. Of the seven populations, only a few individuals in three populations flowered and produced seeds. Vegetative individuals predominated the populations. This skewed distribution of vegetative and reproductive individuals within populations was largely due to herbivory by rodents and cattle that prevented flowering. The surveyed populations showed variability in plant height (38.82±4.39 to 95.37±6.73 cm, p = 0.0001), rhizome length (11.8±0.66 to 27.56±3.74 cm, p = 0.007), number and dimensions of basal and upper leaves, the number of reproductive individuals (0.15 to 2.88 ind. m^{-2}, p = 0.0001) and flower number (16.6±0.67 to 29.12±2.708, p = 0.0001). Breeding experiments confirmed the out-breeding nature of the species and only one insect species foraged and pollinated its flowers. The reproductive output, though relatively more in high elevational populations, was severely constrained by herbivory and pre-dispersal seed predation. Reduced population size, herbivory, reduced number of reproductive individuals, pre-dispersal seed predation and highly-specialized habitat requirements are the major restrictive factors responsible for the present critically endangered threatened status of this species.

Key words: Restricted occurrence, herbivory, out-breeder, rhizome, Kashmir Himalaya, pre-dispersal seed predation

INTRODUCTION

Populations of many plant species, particularly threatened endemic taxa, have sharply declined in the last few decades as a result of habitat destruction, deforestation and overexploitation of some of them for varied economic purposes (Lavergne *et al*., 2005; Colling and Matthies, 2006; Dar *et al*., 2006a, b; 2008). This reduced size alters the population structure and increases the probability of species extinction from demographic, environmental and genetic stochasticity (Bruna and Kress, 2002). Such effects are further exacerbated by spatial isolation of the populations that limits the replenishment of genetic variation through gene flow (Wright, 1969). Degree of out-breeding, in particular, may be severely constrained because small, isolated populations experience reduced pollinator visitation and altered foraging behavior (Byers, 1995; Agren, 1996; Groom, 1998). It is for these important reasons that many workers have investigated different attributes of reproductive ecology of threatened and rare plants, such as flowering frequency and vegetative reproduction (Morely, 1982; Lavergne *et al*., 2005), pollination (Macior, 1978; Karron, 1987; Deyrup and Menges, 1997; Suttle, 2003), breeding system (Planisek, 1983; Karron, 1989; Menges, 1995; Herlihy and Eckert, 2005), seed production and predation (Menges *et al*., 1986; Gisler and Meinke, 1997; Albert *et al*., 2005), seed germination (Baskin and Baskin, 1997; Clark *et al*., 1997; Florance, 1997; Ferriol *et al*., 2006). Such studies have convincingly demonstrated that the study of reproductive ecology is not only pivotal to gaining insight into the factors restraining the size of plant populations, but is also essential for formulating conservation strategies for effective management of threatened species (Bruna and Kress, 2002). It is in this context that the present study was conducted on *Meconopsis latifolia*, a critically endangered endemic angiosperm species in the Kashmir Himalaya, wherein we investigated inter-populational differences in the incidence of herbivory, number of vegetative and reproductive individuals, pollination patterns, reproductive output and pre-dispersal seed predation.

Corresponding Author: A.R. Dar, Department of Botany, Government Degree College (Khanabal) Anantnag, Jammu and Kashmir, India Fax: +91 194 2421357

MATERIALS AND METHODS

This research project was conducted from 2004 to 2006.

Study area: Seven study sites (Table 1), where populations of *M. latifolia* existed, were located in the Kashmir Himalayan region which is situated in the Northern fringe of the Indian subcontinent between 32° 20′ to 34° 50′ North latitude and 73° 55′ to 75° 35′ East longitude and covers an area of about 16,000 sq. km^2. It is formed by a girdling chain of the Himalayan mountains, namely the Pir Panjal range in the south and the Great Himalayan range all along the southeast through northeast to the West. The climate of the Valley is predominantly temperate, changing to sub-alpine and alpine higher up in the mountains. The study sites mostly remained under snow from November to May during which no observations could be recorded.

Study species: *Meconopsis latifolia* Prain (*Blue poppy*, *Guli Neelum*, *Kandyari*) is an endemic monocarpic perennial herb of Papaveraceae and inhabits rock crevices with thin soil, or occur around rocks, or among big boulders in sandy soil at an altitude ranging from 2,800 to 4,000 m (amsl). The individuals of this species remain vegetative for four years and flower during the fifth year. However, flowering can be delayed if the vegetative individuals are damaged by herbivores. The flowering individuals of this species bear a single, erect, unbranched, cylindrical, bristly, hard and grooved stem. About 25 flowers are borne in racemes. Each flower is showy, complete, regular, actinomorphic, hermaphrodite, hypogynous and has a thin, erect, cylindrical, solid, flexible, bristly pedicel. Petals are four, obovate, obtuse, thin or pappery, delicate, soft, with wavy margins, partially transparent and bluish in colour (hence the name blue poppy). Fruit is a many-seeded capsule.

Population density and fate of individuals: A total of 60 permanent quadrats (1 m^2) were established across seven populations immediately after melting of snow in the month of May (sprouting/seed germination) to study population density (numbers/m^2) and fate of individuals. The seedlings after attaining distinctive appearance were marked using colour paint following Khushwaha *et al.* (1981). The marked seedlings were again counted on the subsequent census to record mortality and survival of the individuals. The seedlings without colour marking on each sampling date constituted the new recruitments, which after counting were marked with the colour paint in the permanent quadrats to distinguish between already recruited and new recruits on the successive sampling dates. Marked plants in quadrats were monitored from sprouting to senescence throughout the growing season and census was conducted after every 15 days. The life stage of individuals (reproductive and vegetative), mortality by herbivory, part herbivored and other related details were also noted.

Breeding behavior: For this purpose, 12 plants were randomly selected from the Budhsheri population and 13-23 floral buds on each plant were selected for pollination experiments. Two randomly selected plants were then subjected to one of the following treatments:

- Unemasculated flowers covered with butter paper bags to test for forced selfing (17, 19 buds)

Table 1: Habitat characteristics of the study sites supporting seven different populations of *Meconopsis latifolia* in the Kashmir Himalaya

	Study sites						
Characters	Budhsheri	Harmukh range	Kaan	Lower panchdooni	Lower surkhatch	Upper panchdooni	Upper surkhatch
Altitude	3680 m	3850 m	2950 m	3280 m	3070 m	3460 m	3190 m
Composition	Huge sedimentary rocks	Huge sedimentary rocks or boulders	Small to medium-sized rocks or boulders	Small to medium-sized sedimentary rocks	Huge sedimentary rocks	Medium to large-sized sedimentary rocks	Medium to large-sized sedimentary rocks
Soil	Less deep, very sandy, loose, moist, dark colored	Deep, loose, less sandy, moderately-moist, light-brown	Deep, mixed with small amount of sand, loose, moist, light-brown to dark colored	Deep, pebbled, hard, moist, light-brown	Less deep, less sandy, relatively hard, moderately-moist, dark colored	Deep, pebbled, hard, less moist, light-brown to dark colored	Less deep, less sandy, relatively hard, moderately-moist, dark colored
Species dwells	In crevices, under rocks, in wide caves, or alongside rocks	In very narrow and tight, deep rock crevices, under or among rocks	In narrow and wide rock crevices and among small spaces in, or under boulders	On, among or under, rocks	In narrow and wide rock crevices	On, among or under, rocks	In narrow and wide rock crevices
Exposure	Well-exposed	Well-exposed	Partially shaded to well-exposed	Well-exposed	Shaded	Well-exposed	Shaded
Stability	Least stable	Least stable	Least stable	Less stable	Less stable	Less stable	Stable
Grazing	Frequent	Less frequent	Very frequent	Very frequent	Very frequent	Very frequent	Very frequent

- In order to check for outcrossing ability the unopened flower buds were emasculated and subjected to the following treatments
  - Flowers left open to cross pollinate (20, 23 buds)
  - Emasculated flowers covered with bags and not allowed to pollinate to test for apomictic seed development (18 buds on each plant)
  - Receptive stigmas hand pollinated using pollen from flowers of the same plant to test for geitonogamy (19, 18 buds)
  - Receptive stigmas of several flowers of the same species were impregnated with pollen from flowers borne on different individuals of the same species to test for xenogamy (20, 15 buds)

Emasculations, done with the help of blunt ended forceps, were performed immediately on flower opening to minimize damage to floral organs. Butter paper bags with fine pores were used for bagging purposes. As the plants bloom basipetally, the treatments were established early in season and all the floral buds in bagging experiments were in the top 1/3rd of inflorescence. Bags were removed after the stigmas became completely non-receptive (after approx. 10 days) and the resulting fruits from these treatments were collected. Number of seeds (wherever, formed) per capsule was also recorded.

Floral visitors: Floral visitors to *M. latifolia* were monitored only in three populations located at Budsheri, Harmukh range and Kaan because of the occurrence of flowering individuals only in these populations. An area of 10 m^2 was demarcated in each study site and 36 observation sessions were conducted for 6 days during different times of a day (from 8 am to 6 pm). Each observation session was of 30 min duration. During each observation session, number of visits an insect made, time it spent on one flower, number of flowers it visited in a single visit and the number of plants it visited were recorded. To standardize these observations, we calculated the number of floral visitors per flower on hourly basis as the total number of visitors observed divided by the number of flowers. An insect landing anywhere on the inner petals, pistil or stamen was treated as one insect visit. Visitation rate was calculated as the total number of visits made to each population divided by the number of flowers to yield number of insects per flower per hour. Representative floral visitors were trapped, anaesthetized with NaCN and scrutinized for pollen load on their body parts. The pollinator was identified at the Department of Zoology, the University of Kashmir, Srinagar, J and K, India.

Reproductive output: Ten randomly selected and tagged reproductive individuals were used to gather data about reproductive output. Besides, plant height, number of buds, number of flowers and fruits per plant were also recorded.

Data analysis: Basic statistics, such as trait means and variances and Analysis of Variance (ANOVA) were calculated using SPSS 10. Significance is set at the $p = 0.05$ level.

RESULTS

Population density and fate of individuals: Density of individuals varied significantly across different populations ($p = 0.0001$) (Fig. 1and Table 2) and highest density of 13.2 individuals m^{-2} was recorded in Harmukh range population and lowest of about 1.36 individuals/m^2 in Lower Panchdooni population. Vegetative individuals were predominant and varied significantly across the populations ($p = 0.001$). Reproductive individuals were recorded only in Budhsheri (1.22 ind. m^{-2}), Harmukh range (2.88 ind. m^{-2}) and Kaan (0.15 ind. m^{-2}) populations yet, showing significant variation ($p = 0.0001$). Mortality of individuals in various populations largely because of grazing by herbivores, such as cattle and rodents ranged from 2.71 ind. m^{-2} in Budsheri to 0.12 ind. m^{-2} in Lower Panchdooni (Fig. 1). Insignificant variation ($p = 0.070$) was observed in the number of individuals herbivored in the studied populations.

Variability in vegetative and reproductive traits: The vegetative and reproductive attributes exhibited inter-populational differences (Table 2). Height of the flower-bearing axis, which in turn determines the number of flowers borne by an individual, varied significantly in individuals of different populations. Among the investigated populations, Harmukh range had significantly higher average values for plant height ($p = 0.0001$), number of flowers/plant ($p = 0.0001$) and the rhizome length ($p = 0.007$), compared to Kaan and Budhsheri populations. The individuals in Harmukh range population also had greater number of basal ($p = 0.023$) and upper leaves ($p = 0.024$) than Kaan and Budsheri populations.

Breeding behavior: Through bagging experiments (Fig. 2), it was established that seeds were formed both upon cross-pollination as well as on geitonogamous pollen transfer. However, we did not get any evidence of seed formation either under apomictic or autogamous conditions. Seed number per capsule was (479.25±33.99)

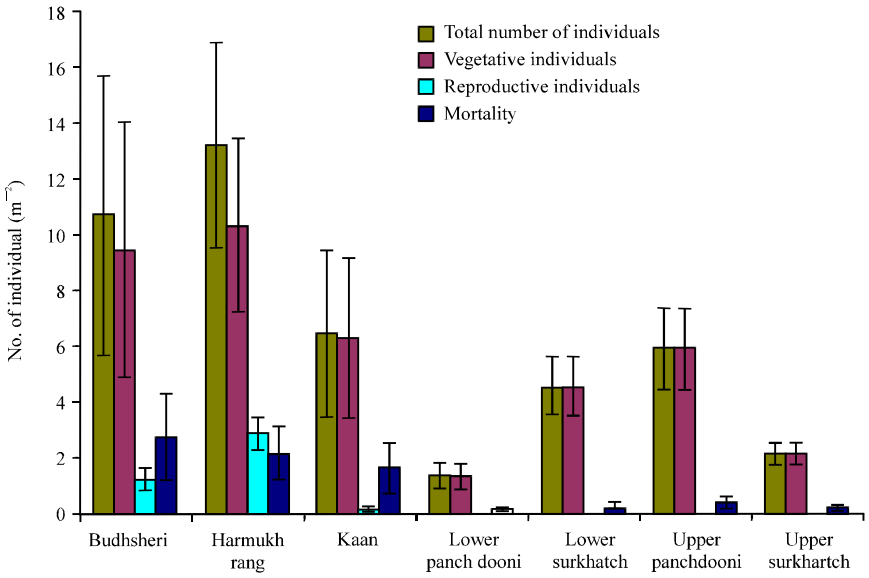

Fig. 1: Comparative demographic details (Mean±SE) of *Meconopsis latifolia* at various populations in the Kashmir Himalaya

Table 2: Results of the analysis of variance testing the differences in various vegetative and reproductive attributes between different populations of *Meconopsis latifolia*

		Results			
Attributes	Source of variation	Mean square	df	F	Sig.
Population density	Between populations	140.96	6	6.33	0.0001
	Error	22.24	53	-	-
New recruits (vegetative)	Between populations	94.70	6	4.47	0.001
	Error	21.17	53	-	-
New recruits (reproductive)	Between populations	6.95	6	28.23	0.0001
	Error	0.24	53	-	-
Total mortality	Between populations	8.66	6	4.97	0.0001
	Error	1.74	53	-	-
Surviving vegetative individuals	Between populations	51.70	6	4.43	0.001
	Error	11.65	53	-	-
Surviving reproductive individuals	Between populations	34.76	6	44.56	0.0001
	Error	0.78	53	-	-
Total number of individuals herbivored	Between populations	3.06	6	0.63	0.70
	Error	4.86	40	-	-
Plant height	Between populations	5119.92	2	18.69	0.0001
	Error	273.85	15	-	-
Rhizome length	Between populations	418.80	2	7.11	0.007
	Error	58.90	15	-	-
No. of basal leaves	Between populations	24.51	2	1.66	0.023
	Error	14.76	15	-	-
No. of upper leaves	Between populations	103.81	2	4.81	0.024
	Error	21.56	15	-	-
No. visits	Between populations	1158.50	2	6.51	0.003
	Error	177.80	51	-	-
No. of flowers visited	Between populations	6436.74	2	11.29	0.0001
	Error	569.87	51	-	-
Visitation rate	Between populations	0.17	2	2.85	0.067
	Error	6.22	51	-	-
Visitation frequency	Between populations	1.16	2	7.27	0.002
	Error	0.16	51	-	-
No. of buds per plant	Between populations	501.70	2	12.03	0.001
	Error	41.69	14	-	-
No. of flowers per plant	Between populations	560.67	2	15.22	0.0001
	Error	36.83	14	-	-
No. of fruits per plant	Between populations	547.26	2	18.34	0.0001
	Error	29.83	14	-	-
No. of predator infested fruits	Between populations	162.05	2	15.18	0.0001
	Error	10.67	14	-	-

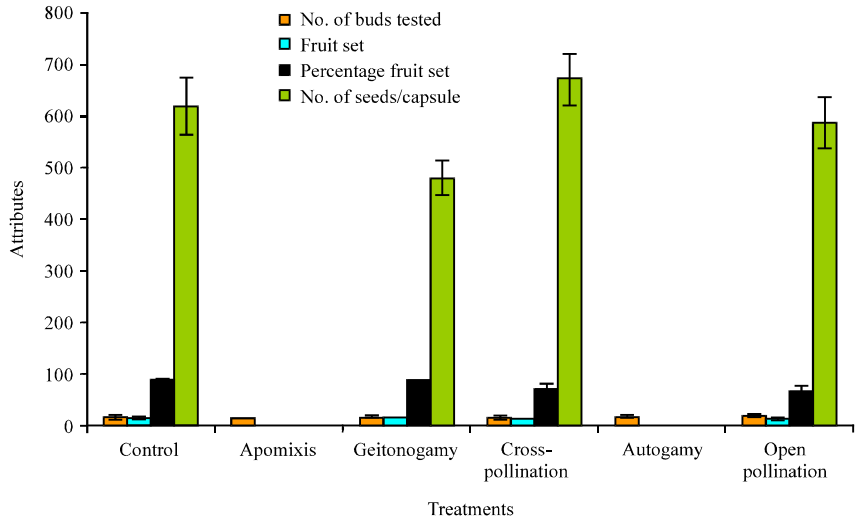

Fig. 2: Breeding behaviour of *Meconopsis latifolia* (Mean±SE) in the Kashmir Himalaya

in geitonogamously-formed capsules and (670.8±48.27) in capsules formed after cross-pollination. Manually cross-pollinated flowers had almost the same seed set (670.8±48.27) per capsule as in capsules formed from unemasculated flowers (tagged for open pollination), where it was 618.25±55.35. Also, 586.95±51.60 number of seeds per capsule were recorded for emasculated flowers left for open pollination as against (618.25±55.35) recorded for control (unemasculated flowers).

Floral visitors and pollination pattern: One insect species (*Bumbus* sp.) of Bombideae visited *M. latifolia* and foraged its flowers in all the seven populations. The pollen load on hind legs and abdomen of the insect was very high, while a limited number of pollen grains were observed on the thorax and front legs. Close observation of the visitation of the insect species revealed that after landing on stigma it enters the central cluster of bright yellow to orange-colored stamens and while it puts its mouth and front legs near filament bases around the ovary, its abdomen and hind legs continuously brush the anthers. Then the insect shifts to the next flower on the same plant, or on the next nearby plant. The *Bumbus* individuals visited the flowers more frequently between 8 am to the noon and then again from 3:30 p.m. till 6 p.m. On average, the insect spent 30-50 sec on each flower that it visited at a time. The frequency of visitation increased with increase in the number of flowering individuals and the number of flowers in a population. The population at Harmukh range had significantly greater number of visits/hour (22.78 ± 4.49, p = 0.003), total number of flowers visited h^{-1} (44.55±8.35, p = 0.0001), visitation rate/hour (0.37±0.07, p = 0.067) and visitation frequency (0.67±0.13, p = 0.002) than the populations at Kaan and Budsheri (Fig. 3 and Table 2).

Pre-dispersal seed predation: All the immature capsules enclosing bright-white ovules were found devoid of any predator. But as the seeds approached maturity, usually in the uppermost capsules of plant, a large number of small (3-7 mm long) insects with dull-white body and faint-red head of the Order Coleoptera, were noticed. These insects had undulating/gliding or creeping movements and were most concentrated towards the basal portion of capsule, from where fertilized ovules start maturing into seeds. Depending upon the number and activity of these insects, the infested portion in many capsules turned into a black dust. These insects were either confined to one portion of the capsule, or occurred in groups within it. The majority of the plants examined in the different populations showed the presence of these insects in their mature capsules. The percentage fruit set was highest for Harmukh range followed by Budsheri and the lowest for Kaan. Also, the number of infested capsules was highest for Harmukh range, followed by Budsheri and Kaan. Percentage seed predation was significantly higher for Harmukh range (p = 0.0001) and lowest for Budsheri population (Fig. 4 and Table 2).

Reproductive output: The number of floral buds per plant was significantly (p = 0.001) higher in the Harmukh range population than in the Kaan and Budsheri populations (Fig. 5 and Table 2). Also the number of flowers in Harmukh range population was significantly (p = 0.0001) greater than Kaan and Budhsheri populations partly

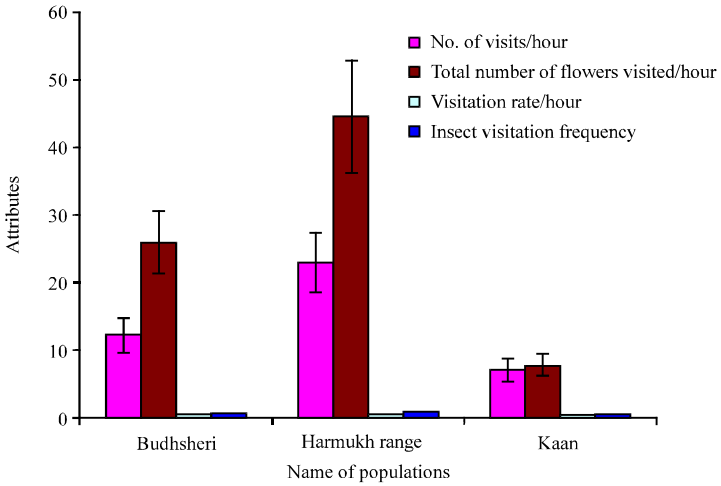

Fig. 3: Insect visitation frequency (Mean±SE) at some populations of *Meconopsis latifolia* in the Kashmir Himalaya

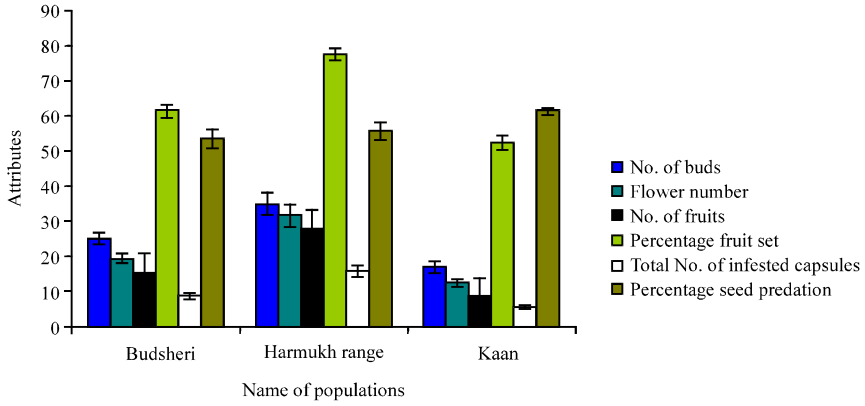

Fig. 4: Pre-dispersal seed predation (Mean±SE) in three populations of *Meconopsis latifolia* in the Kashmir Himalaya

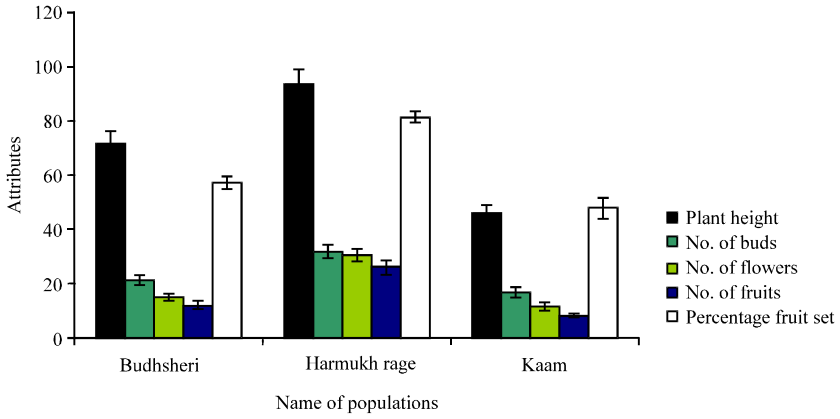

Fig. 5: Reproductive out-put (Mean±SE) of different populations of *Meconopsis latifolia* in the Kashmir Himalaya

because of the browsing of flowers by cattle which also results in lesser percent fruit set per plant in Kaan and Budsheri populations, compared to Harmukh range population ($p = 0.0001$).

DISCUSSION

In *Meconopsis latifolia* a series of events and/or reproductive problems contribute to the decline of the species in a compounding manner. Several ecological factors appear to act, either independently or in concert, leading to an irreversible decline of the species in the Kashmir Himalaya. This narrow endemic species occurs in habitats with a steeper slope, rocky substrate, fewer coexisting species and with very sparse vegetation. This pattern is consistent with the results obtained for other regions, where similar habitats contain numerous narrow-endemic plant species (Baskin and Baskin, 1988; Matthews *et al*., 1993; Wolf, 2001; Lavergne *et al*., 2004). In such habitats, these rare endemic species may incur less aboveground competition and fewer competitive interactions. Besides, in habitats where *M. latifolia* occurs, succession to dense vegetation and forest is probably very slow or even prevented by local edapho-climatic conditions. Thus, these habitats may represent ecological islands (Pigott and Walters, 1954; Maliakal-Witt *et al*., 2005) and may have acted as local refuges for the persistence of such narrow endemic species (Albert *et al*., 2001).

Population size at all the seven study sites of *M. latifolia* was small, consisting of few individuals. The population size in such rare endemic plants is known to be primarily determined by the availability of microhabitat for their successful regeneration (Tilman *et al*., 1994; Hegland *et al*., 2001; Overbeck *et al*., 2003) and availability of microsites for new recruits within these microhabitats. Furthermore, populations were predominated by individuals in pre-reproductive (vegetative) phase because of recurrent herbivory by rodents and cattle hindering their attainment of reproductive competence. Damage upon herbivory was offset to some extent by resprouting, but consistent and persistent herbivory prevented any further growth and such individuals survive as underground rhizomes and sprout only in the next growing season. Thus, the number of individuals capable of reproduction is highly reduced in these populations and the same represents a critical bottleneck for the species to extend its range in the Kashmir Himalaya. Besides, damage and death of the delicate underground perennating organ due to the activity of herbivores further complicates the survival and spread of this highly microhabitat-specialist endemic species. The higher number of individuals in reproductive phase recorded in higher elevational population (as at Harmukh range) is probably due to the inaccessibility of such populations to herbivores, especially cattle. Several other studies have also shown that herbivory dramatically limits seed production (Ayre and Whelan, 1989; Escarre *et al*., 1999), seedling survival and recruitment (Louda, 1982) and ultimately population growth (Ehrlen, 1996). Furthermore, strong impact of herbivory on the reproductive success of these populations may also weaken pollinator-mediated selection on reproductive traits (Levri and Real, 1998) and attractiveness of plants to pollinators as reported by Strauss and Armbruster, (1997) in *Raphanus raphanistrum*. In fact, it has been argued that repeated and persistent herbivory over longer periods of time could have been the major selection force promoting evolution of semelparity (monocarpic perennial) in plants (Klinkhamer *et al*., 1997).

The pollination experiments suggested self-incompatible or cross-compatible nature of *M. latifolia* since seed production was obtained only on geitonogamous and cross-pollination treatments. The out-breeding nature of the species is further ensured by protogynous flower, exserted stigma above anthers, earlier maturation of stigma than anthers and by distinctive spatial separation of the anthers and stigmas. Notwithstanding the out-breeding nature of the species, low frequency of insect floral visitors noticed across different populations could be attributed to fewer numbers of flowers and reduced attractiveness of flowering individuals by herbivore damage as has also been reported by Solbrig and Rollins (1977) in *Leavenworthia* and by Matsumura and Whashitani (2002) in *Primula sieboldii*. Variation in insect-pollinator activity and thus in the rates of pollen transfer, can also strongly limit the number and quality of seeds (Sih and Baltus, 1987; Burd, 1994; Agren, 1996; Charpentier *et al*., 2000), although such an effect may be highly variable in space and time (Baker *et al*., 2000). Except for the Harmukh range population, limited seed production was recorded in all the populations with restricted reproductive individuals. The key factors limiting the production of seeds included less number of reproductive individuals within populations, floral damage by herbivores and perhaps restricted pollinator visitation. Low-seedling recruitment in this species may be caused by low seed production as a consequence of pollinator limitation, seed predation, lack of favorable conditions, or microsites for seedling establishment. Thus, intricate network of factors, such as short favorable growing season, pre-dispersal seed predation, seed dispersal pattern, specific chilling requirements of seeds, favorable soil, moisture and temperature requirements and herbivory have profound effects on the recruitment pattern, mortality, establishment and population size of this species.

In conclusion, herbivore damage, pollination pattern, reduced reproductive output because of pre-dispersal

seed predation, besides local climatic conditions, short growing season and highly specialized habitat (rock crevices and screes) are the key factors that contribute to present critically endangered threat status of *M. latifolia* in the Kashmir Himalaya.

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