

A NORTHERNMOST POPULATION OF *CYPRIPEDIUM CALCEOLUS* L. (ORCHIDACEAE): DEMOGRAPHY, FLOWERING, AND POLLINATION

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ABSTRACT. Above the Arctic Circle, monitoring of a population of *Cypripedium calceolus* was conducted in 1992–1998, and 7-year population dynamics were analyzed. In 1998, experimental work on artificial pollination was carried out. The absence of typical insects for pollination and the short growing period with low temperatures were main constraints to the distribution of this orchid in the northernmost regions.

Key words: Arctic Circle, boreal orchids, Russia

INTRODUCTION

Many constraints limit the range of distribution of a species. Temperature and humidity seem to be the major factors; and, at the distributional limit, the influence of these factors is greatest. Low temperature reduces plant size and seed production at the northern limit of the distribution area for many species (Masurenko 1986, Volder 1999), thus transforming (changing) typical plant behavior (strategy) in biosystems. For insect-pollinated species, the absence of suitable insects might limit the distribution of the species as well. This may result because the distributional range of the pollinator might not coincide with the distribution area of a plant species. Furthermore, because of the shorter growing period in the north, seeds may not ripen or may even remain inside the fruit without being released, thus inevitably reducing the number of offspring in a population.

Cypripedium calceolus L. was the first orchid species to be protected in many European countries, as early as the 19th century (Stewart 1992). Populations of this species are almost extinct in the wild in Great Britain, where *C. calceolus* currently exists only in a single locality (Kull 1999); and it is extinct in Greece (Kalopissis 1988).

Two main approaches have been applied for conservation of this species: habitat protection with legislation based on international criteria and re-establishment of populations from seeds in the wild (Cribb & Sandison 1998, Ramsay & Stewart 1998). Some of the northernmost populations of this species in Europe occur in Murmansk Region (northern Russia). Populations that grow above the Arctic Circle are subject to the constraints mentioned above.

Four questions are addressed in this research: What is the population performance of this species in the north? What are the population dy-

namics over several years? What factors influence the year-to-year dynamics of this northern population? What measures of protection may be applied to this species in the north?

MATERIALS AND METHODS

Species

Cypripedium calceolus is a rhizomatous orchid species. Its horizontal rhizome consists of segments that are rather long-lived, up to ca. 20 years (Serebryakov 1952, Blinova 1995). This explains why rhizomes of this species can be relatively long. Each annual segment consists of 3 internodes with buds. Usually the bud of the last one produces the next shoot. All the other buds remain dormant. Aerial vertical shoots, up to 50 cm high, have 3–4 large green leaves and terminate in a single flower (sometimes two flowers). Seed capsules contain numerous tiny seeds (Moore 1980, Cribb 1997, Kull 1999).

Cypripedium calceolus is an early-summer species. In Central Russia, in Moscow Region, it flowers at the end of May or in early June (Nevskij 1935, Denisova & Vakhrameeva 1978). In Karelia, flowers appear from early to mid June (Dyachkova et al. 1997).

This boreal species has an extensive range from Europe through Siberia to Asia (Moore 1980, Hulten & Fries 1986, Perner 1996, Cribb 1997, Averyanov 2000). It is reportedly a calciphilous species that grows in coniferous and mixed forests (Reinhard et al. 1991, Averyanov 2000) but on light-acid soils with pH 6.3–6.4 in Murmansk Region (Blinova 1995).

Its pollination syndrome, which is specific, was studied in detail by Charles Darwin (1862). Recent studies confirm that flowers are pollinated by females of *Andrena* bees, but species from *Lasioglossum* and *Halictus* genera also can act as pollen vectors (Nilsson 1981).

Study Site

Murmansk Region in northwest Russia (66°–70°N) falls into the Atlantic-Arctic climatic zone of the temperate belt. Because of the Gulf Stream, Murmansk Region has a rather mild climate, causing the dominance of boreal vegetation over tundra. Only in the northern parts and at higher elevations in the Khibiny and Lovozero Mountains are the coniferous forests gradually replaced by birch forests, dwarf shrub, lichen tundra, and arctic deserts (Zinserling 1934, Ramenskaya 1983, Koroleva 1994).

In Murmansk Region, *Cypripedium calceolus* occurs in sparsely forested habitats in light shade, with a canopy openness of ca. 30–50%. The soils are podzols, peaty podzols, and peat soils. Most populations of *C. calceolus* grow in the southern parts of Murmansk Region. All populations are isolated. In the study area, near Apatity, *C. calceolus* occurs in pine forest. Natural plant communities in the region of observation are mainly pine forests of the north taiga type, with *Betula pubescens*, *Salix caprea*, and *Juniperus sibirica* dominating the understory. The herb layer typically consists of species such as *Cirsium heterophyllum*, *Bartsia alpina*, *Potentilla erecta*, *Lerchenfeldia flexuosa*, *Geranium sylvaticum*, *Luzula pilosa*, *Solidago lapponica*, *Melampyrum sylvaticum*, *M. pratense*, *Chamaenerion angustifolium*. The herb layer also includes dwarf shrubs, especially *Empetrum hermaphroditum*, *Vaccinium uliginosum*, *V. vitis-idaea*, and *Calluna vulgaris*.

Fieldwork was carried out in the central part of Murmansk Region, near the city of Apatity, between 1992 and 1998.

Methods

As a result of clonal growth, the population of *Cypripedium calceolus* clearly could be divided into separate subpopulations of different sizes. These subpopulations varied in number of aerial shoots. All recorded shoots were assessed and placed into the following classes, or ontogenetic stages:

Juvenile (*j*).

Individuals having small shoots with 1 or 2 leaves up to 3 cm in length;

Immature (*im*).

Individuals intermediate between juveniles and adults, having shoots with 2 or 3 leaves and a height of 10–15 cm, half that of adult individuals;

Vegetative (*v*).

Individuals including a mixed group with temporary non-flowering shoots and post-im-

mature individuals having shoots of 3 or 4 leaves and a height of 20–40 cm;

Generative (*g*).

Flowering individuals having shoots of 3 or 4 leaves, 1 or 2 flowers, and a height of 30–50 cm; and

Senile (*s*).

Individuals having shoots of 2 or 3 leaves, often damaged, without flowers, and with broader leaves than those in immature individuals.

In addition to separate counts of shoots in each of these ontogenetic stages, counts were made of total number of shoots, flowering shoots, and non-flowering shoots.

The following phenological phases were distinguished:

Pre-flowering.

From appearance above ground until opening of first flower bud;

Flowering.

From the opening of first flower bud until withering of this flower (if two flowers have developed, then until the withering of second flower);

Fruiting.

From the withering of first flower until seed dispersal; and

Dying back.

From first dead leaf until death of the entire shoot.

Phenology of the population was recorded every week from appearance above ground (early June) until seed dispersal and dying back of shoots (September–October).

Data on air temperature and number of frosts during the vegetative period (June–August) and early autumn (September) were collected from the Meteorological Station of the Polar-Alpine Botanical Garden-Institute. The growing period was considered as the duration of time when air temperature rose above 5°C in the spring until it fell below this point in the autumn.

An artificial pollination experiment was conducted. Of 51 flowering shoots recorded in 1998 in the population, 38 flowering individuals of *Cypripedium calceolus* were marked, and a distinguishing number was given to each of them. To estimate the rate of natural and artificial pollination, two parts of the population and two genets were selected. In part of the population, 25 flowers of 23 shoots were artificially cross-pollinated. The cross-pollination was conducted by an application of the whole anther disc from a flower of a neighboring shoot to the stigma of another flower. In another part of the population,

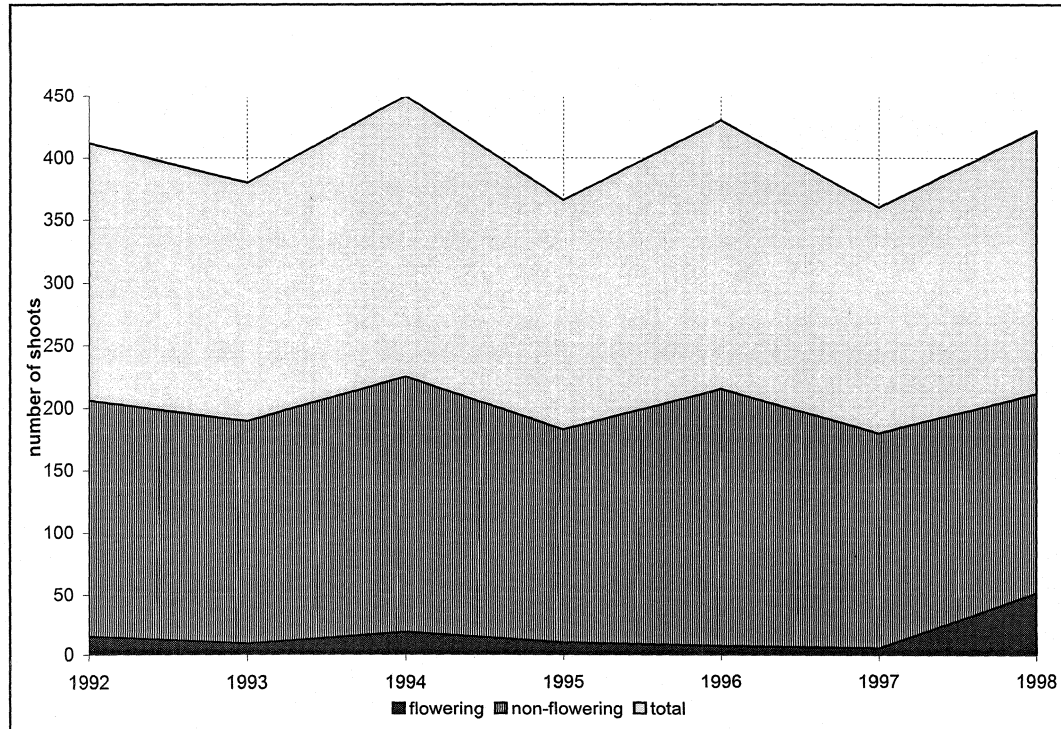


FIGURE 1. Dynamics of flowering and non-flowering individuals in a population of *Cypripedium calceolus* L., in numbers.

15 flowers of 13 shoots were allowed to be pollinated naturally. Two different genets, sharing similar habit, were chosen; and seven flowers of seven shoots of one genet were artificially cross-pollinated. In another genet, 12 flowers of ten shoots were allowed to be pollinated naturally. During the flowering period, all insects found inside the lips of the flowers were collected and identified to species.

RESULTS

Flowering Dynamics

Year-to-year dynamics were observed in the total number of flowering and non-flowering individuals in the population. Permanent fluctuations of both total number of shoots and non-flowering shoots were recorded during 7 years of observation (FIGURE 1). The range of variation, however, was constant between 180 and 225 shoots. Relative and absolute numbers of flowering shoots were extremely low (FIGURES 1, 2). In the 1992–1997 period, the percentage of flowering shoots never exceeded 10%, whereas the percentage in 1998 was very high, viz. 24%.

Ontogenetic Dynamics

Year-to-year dynamics were measured in the recognized ontogenetic stages. Of these five groups, three (juveniles, generatives, and seniles) were represented by very low relative (0–8%) and absolute (0–20) numbers during most years of this study (FIGURES 3, 4). Most fluctuations occurred in the groups of immature (6–24%) and vegetative (67–87%) individuals (FIGURES 3, 4). In 1998, however, a decreased number of vegetative shoots (57%) and an increased number of generative shoots (24%) were noted.

Weather Influences

Influences of weather conditions were measured during the 7-year study.

Air temperature.

The growing period lasted 4 months from mid-May until mid-September. The long-term mean of air temperature varied from June to September: 8.8°C in June, 13°C in July, 10.2°C in August, and 5.1°C in September (FIGURE 5). As seen in FIGURE 5, air temperature differed considerably from year to year. Only the 1994

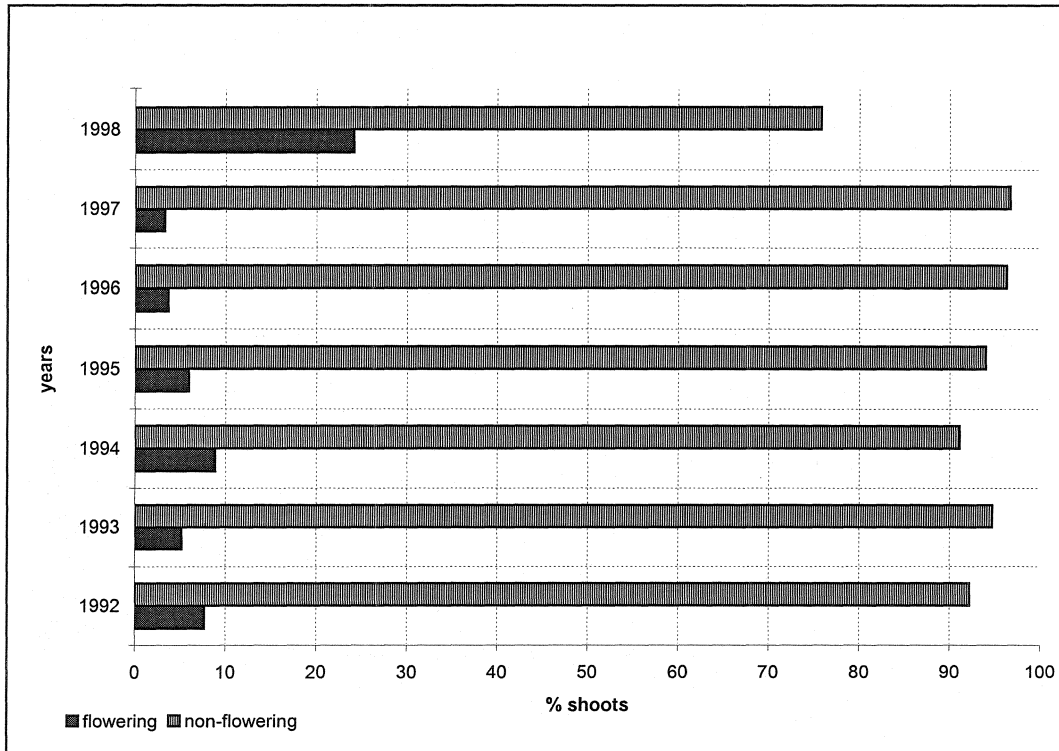


FIGURE 2. Dynamics of flowering and non-flowering individuals in a population of *Cypripedium calceolus* L., in percentages.

mean more or less matched the long-term mean; and 1997 was extremely warm with an average temperature of 14.2°C in July and 11.5°C in August. Low mean temperatures in July (8.8°C) and August (7.2°) were recorded in 1992 and in June (6.1°C) and August (6.7°C) in 1996. Both these years were rather cold. Mean temperatures in September were extremely low (−0.2°C) in 1996 and relatively high (6.9°C) in 1992.

Frosts.

According to long-term climatic data, about 15 frosts can be expected during the growing period (FIGURE 6). Most of them occur in September. The number of frosts in 1992–1998 varied from 5–30 and differed from long-term mean observations. Record numbers of frosts occurred in September 1993 (22) and in September 1996 (20).

Phenology

Development of vegetative and reproductive structures of this species lasts for 17 weeks in the region of observation, from early June until early October. The species flowers for ca. 10 days. The duration of fruiting and ripening of

seeds lasts quite a long time, from mid-July until early October. Seed dispersal takes place after the first week of October. The following data were collected: pre-flowering time, June 1–July 7 (37 days); flowering time, July 7–July 15 (8 days); fruiting time, July 15–October 8 (85 days); and dying back time, September 3–October 8 (35 days).

Pollination

Pollination studies conducted on a part of the population produced the following data (TABLE 1, A):

Artificial cross-pollination.

With 25 flowers from 23 shoots pollinated, 23 seed capsules developed (92%). Capsule size was 3.0–4.5 cm × 1.3 cm, and the number of seeds per capsule averaged 4287.

Natural pollination.

When 15 flowers of 13 shoots were allowed to be pollinated naturally, five seed capsules resulted (33%). Capsule size was 2.5 × 0.5 cm. The average number of seeds per capsule was 1423.

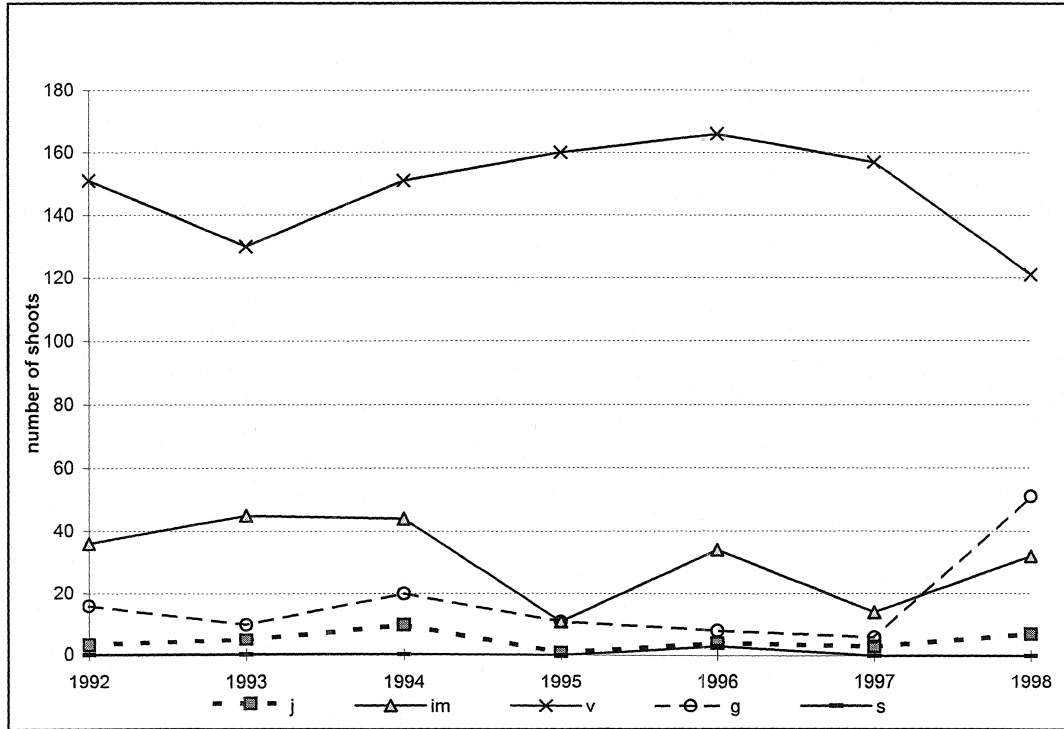


FIGURE 3. Dynamics of ontogenetic stages in a population of *Cypripedium calceolus* L., in numbers; j = juveniles, im = immatures, v = vegetatives, g = generatives, and s = seniles.

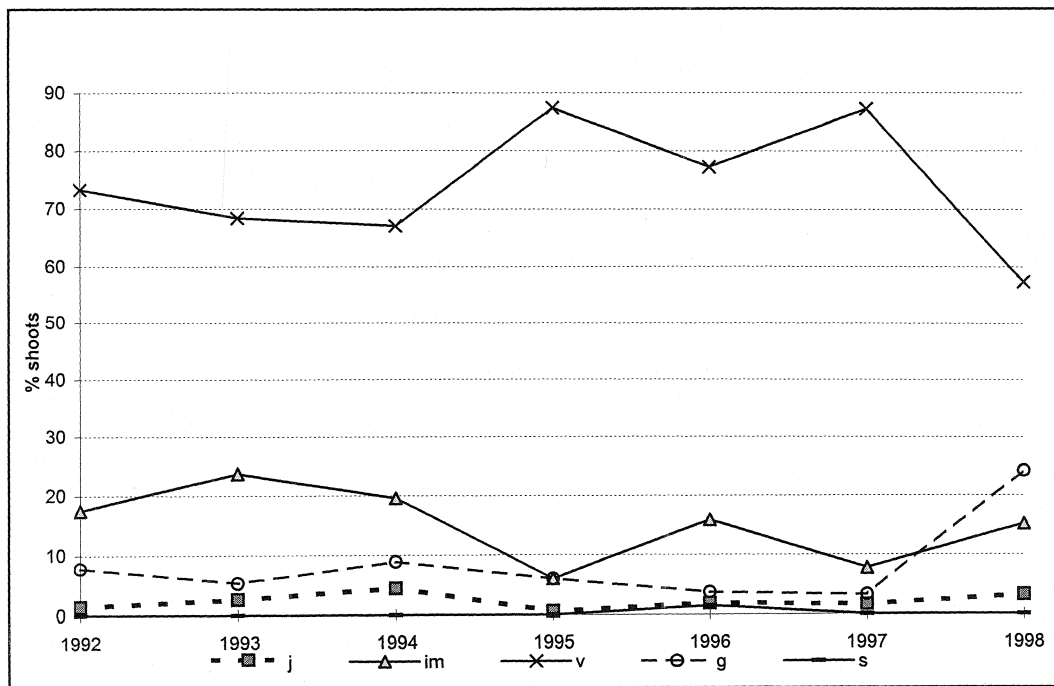


FIGURE 4. Dynamics of ontogenetic stages in a population of *Cypripedium calceolus* L., in percentages.

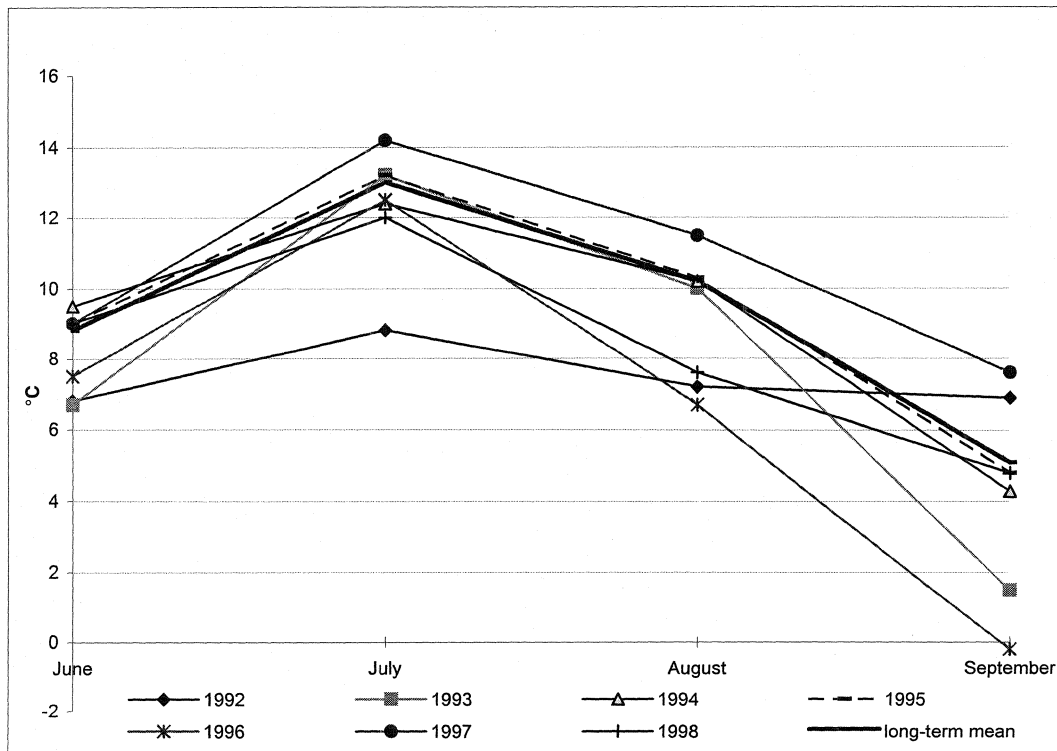


FIGURE 5. Air temperature in Murmansk Region, 1992–1998 and the long-term mean.

Pollination studies conducted on a genet of the population produced the following data (TABLE 1, B):

Artificial cross-pollination.

In genet N6, a total of seven flowers of seven shoots gave seven seed capsules (100%). The average height of shoots in this genet was 40.43 cm.

Natural pollination.

In genet N3, a total of 12 flowers of 10 shoots produced four seed capsules (33%). The average height of shoots in this genet was 34.6 cm.

All the insects observed were flies from the family *Syrphidae*: *Syrphus* sp. and *Eristalis* sp. Only once has an *Andrena* bee been found among insect collections from Murmansk Region during the flowering time of *Cypripedium calceolus*.

DISCUSSION

Population fitness is estimated as the number of offspring left in succeeding generations (Harper 1977, Cooper 1984). These new descendants can be both of sexual and non-sexual origin. New plants of sexual origin (genets) intro-

duce new genetic material into a population, whereas new individuals of non-sexual origin (ramets) are identical to an existing genotype in a population. Based on the adaptive responses of plants in a specific environment, different plant strategies are described (Grime 1979, De Kroon & Schieving 1990, De Kroon & Groenendaal 1990).

Considering a balance between vegetative and generative multiplication, the author distinguished three scenarios in which populations might profit in particular environmental conditions. Populations of some plant species (*Dactylorhiza* spp., *Diphelypaea coccinea*) may benefit by producing enormous amount of seeds and relatively low vegetative multiplication. Other equally prosperous plant populations produce many vegetative offspring and have few flowering individuals that may produce seeds (*Goodyera repens*, *Potentilla anserina*). High fitness in many other populations is achieved by a balance of both new ramets and new genets (*Cypripedium calceolus*, *Convallaria majalis*, *Polygonatum multiflorum*).

A stable strategy for a species may differ at the edges of its distribution area. In European populations of *Cypripedium calceolus*, a certain

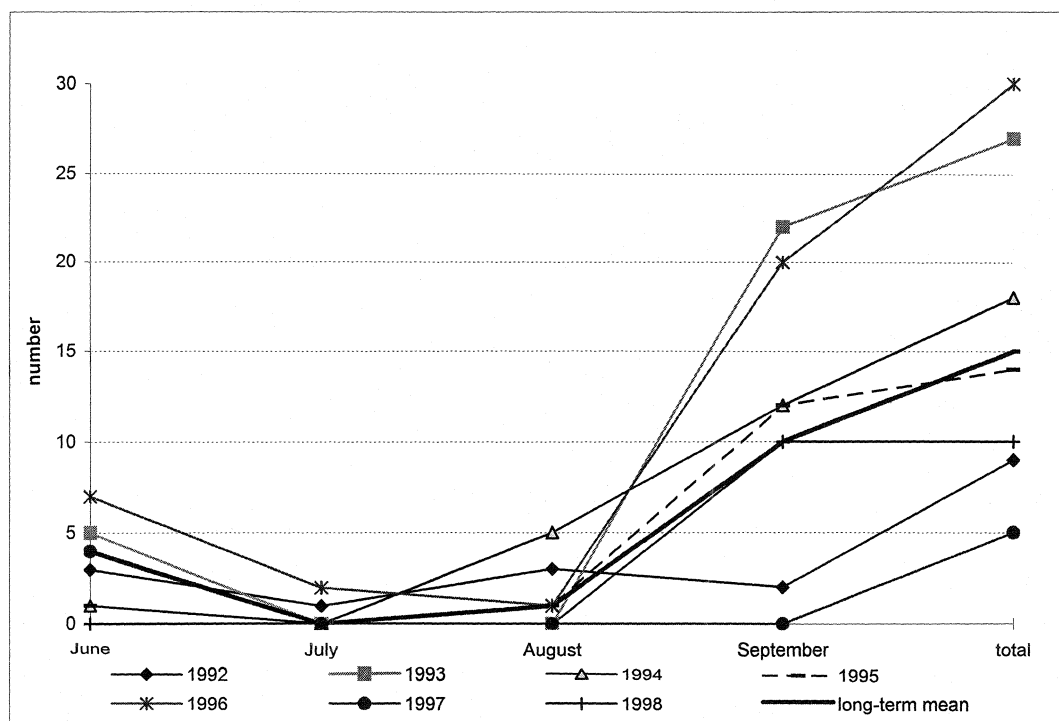


FIGURE 6. Early frosts in Murmansk Region, 1992-1998 and the long-term mean.

balance between vegetative and generative multiplication exists. Kull (1995a) showed that genet dynamics had less fluctuation than ramet dynamics in Estonian populations, with the percentage of flowering ramets varying from 35 up to 71% in different years (Kull & Kull 1991). As a rule, fruit set is reduced compared to flower set. In Estonia, fruit set was 6.8-21.2% (Kull 1995b); in White Russia, it was 33-57% (Stavrovskaya 1984); and in Moscow Region, it was 4-14% (Varlygina & Matsenko 1987). Vegetative multiplication may occur every year with the development of two new shoots: one from the innovation bud and another from the dormant bud (Kull & Kull 1991, Blinova 1995). Even though each capsule may contain up to several thousand seeds, new seedlings are rather rare because of difficulties in germination.

In the northern population of *Cypripedium*

calceolus studied here, both vegetative and generative multiplication appeared to be extremely reduced. Vegetative reproduction was never observed, which explains why all clones of this species studied were linear and never branched. The percentage of flowering shoots was often 3-9%, almost 8-10 times lower than in Estonia. Fruit set was close to zero in many years, hence much lower than in populations of this species in Estonia, White Russia, and Central Russia. Consequently, both sexual and non-sexual processes are extremely reduced above the Arctic Circle.

Low numbers of flowering shoots are probably linked to low temperatures during the growing period. Early frosts may damage flowers in bud. This is exactly what happens to populations of *Cypripedium calceolus* in the north. Dead rudimentary flowers are visible in early summer at

TABLE 1. Results of pollination in the population of *Cypripedium calceolus*: A = part of population, B = genet of population.

Pollination type	Flowers/shoots		Developed capsules	
	A	B	A	B
Artificial cross-pollination	25/23	7/7	23	7
Natural pollination	15/13	12/10	5	4

the top of shoots. In 1994, the number of generative shoots together with shoots with dead flowers was 73 (32.4%), whereas the actual number of flowers was only 20 (9%).

Comparison of the number of frosts and temperatures over several years has shown a strong correlation between these parameters in September and the number of flowering individuals in the following year. In 1998, for example, following the fairly warm September of 1997, which had the lowest number of frosts and the highest air temperature of the recording period 1992–1997, the number of generative shoots developed was 51, the maximum among years of observation. In Murmansk Region, flower buds are formed in September, at the end of growing period, and new snow cover develops by mid-October. Thus the period between the end of August and mid-October corresponds to the period having the most harmful impact of lower temperatures and frosts; because at this time, new flower initials and new buds that will develop into the next shoots are already preformed in the parts of the plant seen above ground. Not only the buds but the new growths also may be damaged during this period. Apparently the variation in total number of shoots reflects these problems in development.

Nectarless orchids have less reproductive success than nectariferous orchids (Neiland & Wilcock 1998). Because *Cypripedium calceolus* does not provide any reward for pollinators, except for a slight fragrance, pollination of this species is often low even in areas of high availability of pollinating insects. Only once has an *Andrena* bee been found in the insect collections made in the central part of Murmansk Region. G.A. Anufriev found an *Andrena* bee in 1998 but not in the area where the population of *C. calceolus* grows. In general, the insect fauna of the region is largely unstudied. The presence of only a few populations of *C. calceolus* and the extreme rareness of potential pollinators explain the low percentage of pollinated flowers, very often close to zero. *Andrena* bees likely are not the pollinators of *C. calceolus* in the north. In Denmark, *Andrena* species were not as effective pollinators as species of *Halictus* and *Lasioglossum* (Erneberg & Holm 1999).

All insects found in the flower lips in Murmansk Region belonged to the family *Syrphidae* (*Diptera*). Nilsson (1981) did not consider these insects as actual pollinators of *Cypripedium calceolus*. In the North, however, these flies may be capable of carrying pollen and act as non-specific pollinators. Several North American cypripediums are reported to be possibly myophilous (Christensen 1994). In our experiments, seed capsules produced by natural polli-

nation were half the size of those produced by cross hand-pollination. If *Syrphidae* accomplish self-pollination by occasionally carrying some pollen when they are inside a flower lip, this may explain the reduction in capsule size and seed set.

Studies on relationships between pollen load and seed set were conducted in Canada using three orchids, including *Cypripedium calceolus* (Proctor & Harder 1994). They clearly showed that increasing the size of the pollen mass (such as $\frac{1}{4}$, $\frac{1}{2}$, and 1 anther) on the stigma also produces higher seed production. Furthermore, their natural seed set (1495) was less than half that achieved by applying an anther (3478) and was even less than that by adding a $\frac{1}{4}$ anther. In the population of *C. calceolus* studied here, the seed set after natural pollination was 1423 seeds per capsule; after hand cross-pollination, by application of the entire anther, it was 4287 seeds per capsule. Although we used different methods for counting numerous tiny seeds, our data confirm the Proctor and Harder view that loading smaller amounts of pollen causes lower numbers of seeds per capsule.

To germinate, seeds have to fall on the soil. In the northernmost population of *Cypripedium calceolus*, seed dispersal occurs in mid-October almost at the same time as the new snow cover develops. The timing of seed dispersal appears to be another hazard affecting the fitness of this population. In combination, the relatively low temperatures during the growing period and frosts in September, the shorter vegetation period above the Arctic Circle, and the limitation of potential pollinating insects constitute the main constraints that prevent the distribution of *C. calceolus* further north. These constraints result in a gradual erosion of the fitness of the population: firstly by a reduction in the number of flowering shoots, secondly by a reduction in the number of fruits, and thirdly through late seed dispersal.

Efforts to protect populations of *Cypripedium calceolus* must take into account all of the aspects demonstrated in this study. Covering the new growths (such as buds emerging above ground) with pine branches, for instance, may prevent damage to premature flowers and buds; artificial cross-pollination can greatly increase the number of seed capsules and seeds. In addition, germination can be promoted by artificially opening green capsules 4 weeks after pollination and placing them into the soil near mature clones. At that time, young seeds germinate even better than old-ripened seeds (Kulikov 1995). Such measures, applied in nature reserve areas, may enhance the survival possibilities for *C. calceolus* populations in the north.

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