

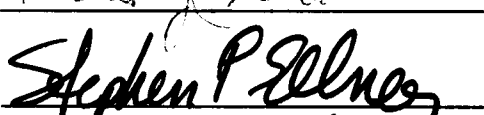
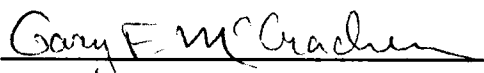
To the Graduate Council:

I am submitting herewith a dissertation written by Margaret Elizabeth Cochran entitled "Consequences of Pollination by Chance in the Pink Lady's-Slipper, Cypripedium acaule." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology.



T. G. Hallam, Major Professor

We have read this dissertation
and recommend its acceptance:



Accepted for the Council:



Vice Provost
and Dean of the Graduate School

CONSEQUENCES OF POLLINATION BY CHANCE IN THE PINK
LADY'S-SLIPPER, CYPRIPEDIUM ACAULE

A Dissertation
Presented for the
Doctor of Philosophy
Degree
The University of Tennessee, Knoxville

Margaret Elizabeth Cochran

March 1986

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DEDICATION

This work is dedicated to my parents, Jim and Elizabeth Cochran, without whose continuing support and assistance my achievements would not have been possible.

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In the course of conducting the dissertation research numerous persons have assisted me greatly. In particular, I would like to thank J. P. Cochran, E. W. Cochran, C. L. Hom, T. King, and B. J. Victor for their invaluable assistance in collecting the field data. Special thanks are also given to the following persons who assisted me in locating populations of pink lady's-slippers for study: N. Coile, The University of Georgia; C. Douglas, Clemson University; D. Pittello, Western Carolina University; T. Patrick, The University of Tennessee, Knoxville; and P. White, National Park Service. Professors M. L. Pan, L. E. Klostermeyer and C. D. Pless assisted in identifying the insect specimens. The Evolutionary Ecology Group at The University of Tennessee, Knoxville, especially J. B. Anderson, C. L. Hom, T. King and D. Urban, provided much encouragement, enthusiasm for ecological research and thoughtful criticism of my work. Thanks also go to M. R. Daunis for proofreading an earlier draft of the manuscript and to C. L. Hom for drawing the maps and flower diagrams. Finally, I would like to thank the members of my committee—Professors E. E. C. Clebsch, S. E. Ellner, L. J. Gross and G. F. McCracken—and my major professor, T. G. Hallam, for their encouragement and their assistance in sharpening my thinking and writing. Whatever errors remain in my work are my sole responsibility.

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ABSTRACT

Pollination is potentially a critical step in the reproductive cycle of angiosperms. Pollinators may act as a mechanism for selection in pollen or pollinator limited plants. The connection between life history, pollination syndrome and long-term fitness was studied in the pink lady's-slipper, Cypripedium acaule. This orchid species has several traits which make it an interesting subject for such a study. These include: a specialist pollinator; no free nectar or other apparent reward; low pollinator visitation; low fruit set; and clonal growth.

Three types of data were collected. A single population of approximately 2000 individuals was monitored from 1982 to 1985. Recruitment, mortality, individual size, flowering and fruit set was recorded each year. Regional variation in fruit set was assessed by sampling populations in Tennessee, North Carolina, South Carolina and Georgia in 1984 and 1985. Finally, the relative intensities of pollinator limitation and resource limitation and their impact on flowering and fruit set were studied by experimentally manipulating populations in the field. Hand pollinations were performed in 1984 and 1985. Defoliation experiments were conducted in 1984 and nectar additions were performed in 1985.

Only a small fraction of either the mature ramets or mature genets flower in a given year. The probability that a ramet will produce a flower increases with ramet leaf area. Pollinator visitation which results in pollinia removal is low, generally including about 20% of the flowers produced. Fruit set is also low, occurring in about 10% of the flowers produced, and is variable from year to year. Reproduction is limited by pollinators, resources

and nectar, but pollinator limitation has the greatest long-term influence on reproductive success.

A game-theoretic model of the effect of nectar on pollinator attraction and fruit set was developed. This model was used to examine how different pollinator foraging schemes may influence the reward offered by plants. In particular, the model predicts that under some foraging schemes, the plant species should produce no reward.

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CHAPTER 1

INTRODUCTION

The study of life histories is concerned inherently with the processes of reproduction and mortality. For ease of study most early investigations of plant life histories focused upon annuals and biennials as opposed to perennials, but as knowledge of plant life histories has grown, ease of study has ceased to be the major consideration in the choice of study organism and researchers have focused increasingly on expanding the types of strategies investigated and on looking for trends across taxa (e.g., Grime 1977, Newell and Tramer 1978, Primack 1979, Bierzychudek 1982a, Wiens 1984, Cruden and Lyon 1985, Fox 1985). The recent interest in perennial herb species has resulted in a number of studies concerned with the consequences of reproductive strategies such as dioecy (e.g., Meagher 1982, Meagher and Antonovics 1982), sex changing (e.g., Bierzychudek 1982b), and clonal growth (e.g., Bishop and Davy 1985, Jurik 1985, Pitelka et al. 1985) over the life span of individuals.

Perennial life histories may include patterns not seen in annuals or biennials. Fluctuations in reproductive success between growing seasons (short-term effects) may be unimportant to an individual's total fitness when averaged over the life span of the individual (long-term effects). Thus, in perennial species hypotheses about the evolutionary consequences of life history traits should be based on long-term rather than short-term effects. Many species of perennial plants occur naturally in populations with a few dominant individuals and many suppressed ones (Harper 1977). For these species, life history traits represent an individual's potential; the extent to

which that potential is attained is determined by environmental factors and interactions with other organisms (Chapman 1928, Cole 1954). The realization of these traits can be summarized by studying a species on the population level. For example, the demographic structure of populations may limit the potential reproductive interactions between individuals (Stearns 1980) and may determine the breeding system of a species to a greater degree than internal mechanisms under individual control such as self incompatibility or the selective abortion of ovules.

Pollination is potentially a critical step in the reproductive cycle of angiosperms and is a major influence on plant breeding systems. Pollinators may act as a mechanism for intense selection in pollen limited plants. The adaptive significance of various floral traits in the orchids and their associated pollination syndromes was examined extensively by Darwin (1877). However, despite numerous studies conducted since then on a wide variety of angiosperm species (for reviews, see Faegri and van der Pijl 1966, Little and Jones 1983, Real 1983) and a renewed interest in the theoretical aspects of sex allocation and breeding systems in plants (e.g., Levin 1979, Charnov 1982, Willson and Burley 1983), the connection between life history, pollination syndrome and long-term fitness has seldom been addressed. The pink lady's-slipper, Cypripedium acaule Aiton, has several traits which make it an interesting subject for such a study. These include: a specialist pollinator; no free nectar or other apparent reward; low pollinator visitation; low fruit set; and clonal growth. Intuition suggests that when a species fails to reward its pollinators, one of the following should occur: the pollinators evolve to avoid the plant species and the plant must evolve another pollination system (e.g., wind pollination, selfing or apomixis) or become

extinct; or the plant species must evolve to offer a reward sufficient to prevent the development of avoidance in at least one of the pollinator species. Nevertheless, many nonrewarding plant species are chiefly or totally insect pollinated. Some of these species attract their pollinators by mimicking rewarding species. However, other species seem to rely upon rare chance encounters with pollinators for pollination (Stoutamire 1971). Cypripedium acaule does not appear to mimic any other concurrently flowering sympatric species, but the nectarless state of the pink lady's-slipper does not seem to have been disadvantageous. In fact, all other members of the genus, along with numerous other orchids and many other plant species, seem to persist with pollination by chance.

This study has several general goals related to clarifying the interaction of life history strategies and pollination ecology. These are:

1. Quantification of the reproductive dynamics of a perennial herb under field conditions, including estimates of pollinator visitation and fruiting success in several habitats.
2. Determination of the relative importance of pollen, resource and nectar limitation of reproductive success through experimental manipulation of individuals.
3. Prediction of the long-term effects of pollen and resource limitation on reproductive success.
4. Investigation of variation in size and stage class distributions within a population and through time, from which the predictability of population dynamics may be determined.
5. Theoretical examination of pollination by chance and its evolutionary implications.

The pink lady's-slipper may be one of the most readily recognizable representatives of the orchid family in the eastern United States. It has long attracted the attention of wild flower enthusiasts, despite the fact that most efforts to transplant this species are unsuccessful. Little is known about its life history or demography, due in some part to the logistical difficulties inherent in its propagation. Seed germination is difficult to induce, the developing plants are slow-growing and take many years to mature, and their extensive root system requires a large amount of lateral space. Despite these problems, C. acaule has many features which make it well suited for long-term study. Due to its conspicuousness, individuals are easy to locate in the field. Its growth form is simple and distinctive and clones are relatively easy to distinguish from independent individuals. Seedlings may be identified to species as soon as they emerge. Pollen is presented in two discrete pollinia, the removal of which is easy to recognize. The large size of the flower eases manipulation of nectar levels and pollinia. Thus, the pink lady's-slipper will be used to examine the long-term consequences of producing no nectar or apparently any other pollinator reward in an entomophilous plant.

This dissertation is organized as follows. In Chapter 2, I describe the natural history of Cypripedium acaule and discuss previous research on this species. Chapter 3 explores the demography of a single population, with emphasis on the influence of leaf area on reproduction and the individual's ability to survive. The pollination ecology of this species is examined in more detail in Chapter 4, including experimental treatments quantifying the extent to which resources, pollinator visitation and the lack of nectar limits the number of flowers which set fruit. In Chapter 5, a game theoretic model is used to explore pollinator foraging schemes and plant characteristics which

may permit nonrewarding species to evolve and persist. In Chapter 6, I present a synthesis of the natural history, demography, and pollination ecology of Cypripedium acaule with theoretical results of the model and offer some predictions about the population dynamics of this species.

CHAPTER 2

NATURAL HISTORY

The Orchidaceae is one of the largest families of monocots, with an estimated 20,000 to 25,000 species (Dressler 1981). Only the Compositae may surpass it in diversity. Although numerous tropical species (particularly epiphytes) have not been catalogued, the systematics of the temperate terrestrial species are well known. The genus Cypripedium L., the lady's-slippers, has been the subject of much popular interest. The pouch-like flowers of these species are the largest and most conspicuous of the temperate orchids of North America. The genus occurs only in the Northern Hemisphere, with eleven species, several varieties, and occasional hybrids found in North America (Brackley, 1985).

Description

Cypripedium acaule, the pink lady's-slipper, consists of two strongly ribbed, pubescent, basal leaves arising from a short rhizome with fibrous roots. The single large, pouchlike flower, usually pink with darker veins but occasionally white, is surrounded by three yellowish green to greenish sepals and a floral bract. The petals exude a sweet fragrance. The lip is fissured with edges folded deeply inward, giving access to the reproductive structures (Figure 1). Pollen is borne on either side of the stigma in two masses, the pollinia, but is loose and granular. Like the other members of this genus, C. acaule produces no nectar or other reward for its pollinators. One possible exception in the genus are the hairs within the labellum of C. calceolus which

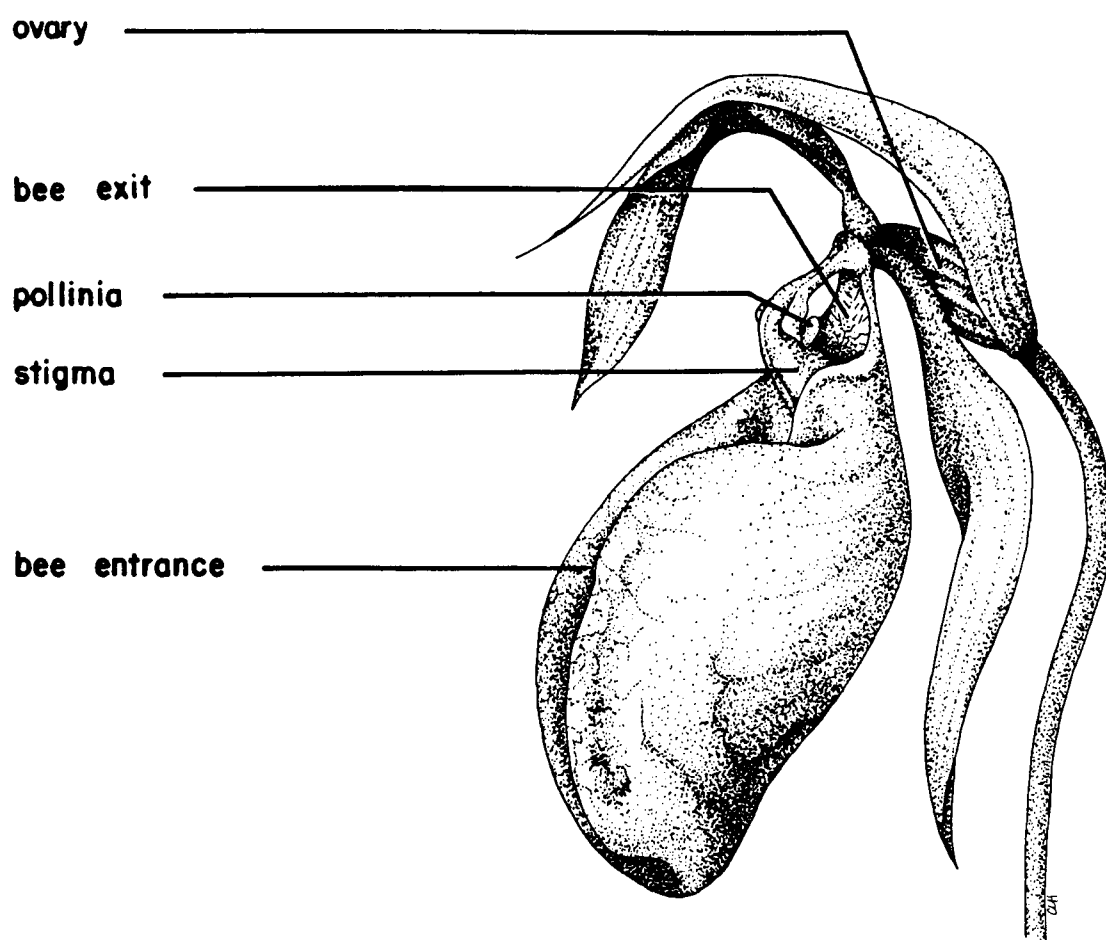


Figure 1: The floral structure of Cypripedium acaule.

were first thought to be covered with nectar (Muller 1883) but which are actually covered with drops of an oil which is also secreted by the leaves (Nilsson 1979). A major component of this oil, a methylanisole isomer, is produced by the roots, leaves and stems of several Cypripedium species, including C. acaule, and may be a defense mechanism protecting the root system and above ground parts (Holman 1983).

The pink lady's-slipper was first described by William Aiton in 1789 (in Aiton 1813). It differs sufficiently from the other members of the genus that it was briefly assigned to the genus Fissipes by Small (Britton and Brown 1936). C. acaule is the only Cypripedium with basal leaves. The cleft in the inflated lip is a longitudinal fissure rather than the rounded opening found in most other species of the genus. The stigma differs in that it is sticky and grooved rather than simply covered with tiny barbs for scraping the pollen off insect visitors (Luer 1975).

The pink lady's-slipper is a trap flower whose size makes it morphologically suited for pollination by large bees. Upon entering the pouch, the bee cannot leave the flower until it brushes past the stigma and one of the pollinia (Figure 1). Occasionally a pollinator fails to find the exit on the first attempt. It may crawl backwards under the stigma and self-pollinate the flower before finding the exit (Macior 1974). However, due to floral morphology, the plant is for the most part an outcrosser. If the bee is of appropriate size, pollination is achieved on its next visit to a pink lady's-slipper when the bee must once again pass under the stigma on its way out of the trap, brushing off the pollen and picking up a new pollen load. Bumblebee queens (Bombus spp.) have been reported as the principal

pollinators (Stoutamire 1967, 1971) but I have observed one successful pollination by a leaf cutter bee (F. Megachilidae).

Distribution

C. acaule is found in eastern North America, ranging from Newfoundland and Manitoba, south along the Appalachian Mountains to the fall line of the Piedmont, and west to northern Indiana, northern Illinois, and Minnesota. Restricted to acidic soils, it commonly grows in dry habitats (Luer 1975) but may also survive in the North at the edges of sphagnum bogs, possibly as relicts of larger populations which slowly decline as the canopy closes (Stuckey 1967). Growth may be stimulated following brush fires, due either to increased nutrient or light availability (Stuckey 1967). In the southern extreme of its range, this species grows in disturbed xeric woodlands and may be locally abundant.

Phenology

C. acaule breaks dormancy in early spring. Full leaf extension and flowering usually occur before the canopy closes. Late frost may destroy buds or flowers but does not damage leaves (Luer 1975). The species is not capable of compensatory growth following frost or herbivore damage. Flowering extends over a 4 to 6 week period, depending on local weather conditions. In this genus, ovules are present at anthesis (van der Pijl and Dodson 1966). Individual blossoms may remain open to pollinators for up to 3 weeks; however, following successful pollination the flower withers more quickly (Plowright et al. 1980). Capsule development is apparent within one to two weeks after pollination has occurred. Although juveniles (individuals

not yet capable of flower production) may go dormant during periods of summer water stress, adults usually maintain their above-ground structures into September and October. The buds for the next growing season's shoots and flowers are formed in the late fall. Capsules do not ripen until fall and may retain some seeds until the next spring. Both the sturdy fruiting stems and the less substantial stems of non-fruiting flowers persist into the next spring.

Life History

As in most orchid species, the seeds of the pink lady's-slipper are small and contain no endosperm. In nature, germination and subsequent establishment is dependent upon the formation of a mycorrhizal association with an appropriate fungus. To be successful, seeds must disperse to locations where they will come into contact with these fungi (Withner 1959). In general, evidence that the mycorrhizal association is species-specific is inconclusive (e.g., Curtis 1939, Harvais and Hadley 1967, Hadley 1970, Withner 1974) and attempts to isolate the species of fungi involved in germination and protocorm development from the roots of mature C. acaule plants have not been successful. Apparently the plant may develop chemical defenses against mycorrhizal infection after it becomes photosynthetically active (Curtis 1939). It is not known if mature plants benefit from mycorrhizal fungi (i.e., Whitlow 1983). Asymbiotic germination has been stimulated on artificial media in complete darkness (Stoutamire 1974), and under these conditions, light appears to prevent germination. Other treatments, such as abrading the seed coat (Devlin in Stoutamire 1974) or boiling the seeds (Arditti 1982) also may be effective at inducing germination. However, these

methods have not elucidated the circumstances under which C. acaule germinates in the field.

In general, following germination, a developing orchid seedling forms a protocorm and gains size by receiving fixed carbon as sugars or other compounds from the mycorrhizal associate (e.g., Smith 1966, 1967; Hadley and Williamson 1971). It may receive other nutrients as well from its mycorrhiza. It is not known if the fungus benefits from the association. Some species of orchids act strictly as parasites on the fungus and experiments with C^{14} labeling have failed to demonstrate translocation of photosynthate from mature orchids to their mycorrhiza (e.g., Hadley and Purves 1974). Many species of orchid endophytic fungi are pathogenic to other plant species (Withner 1974) and a delicate balance must be maintained between the two symbionts. If the fungus spreads too rapidly, parasitism of the protocorm may occur (e.g., Knudson 1925, Hadley 1969).

The protocorm stage may be as short as two years for lab germinated C. acaule seeds (Stoutamire 1974). Withner (in Sanford 1974) estimates that this stage lasts 10-15 years for pink lady's-slippers in natural populations, although Curtis (1943) estimates that a seedling may reach blooming size in just ten years. In any case, the early stages of development are lengthy.

The first aerial shoot produced consists of a single leaf. Plants may remain in this stage of development for several years, producing increasingly larger leaves each year. New rootlets are produced at a rate of about two a year and persist for up to two decades, giving some indication of plant age (Curtis 1943). As plants mature, they eventually reach the adult growth form and produce two leaves.

Flowering occurs in larger plants, although not in a regular pattern (Johnson 1926, Curtis 1954). Fruit set is rare; generally, each season less than 10% of the flowers in a population set fruit (Plowright et al 1980; Brackley 1985). However, each fruit produces thousands of propagules; a ripened capsule may contain 14,000-54,000 seeds (Ricker in Withner 1959) which is similar to seed set in other members of the genus (Stoutamire (1964) reported as many as 54,180 seeds per capsule). Older plants growing in good sites may produce additional shoots to form clumps. Each two leaved shoot is capable of producing a flowering stalk. A multi-flowered individual may successfully set more than one fruit.

CHAPTER 3

DEMOGRAPHY

The population dynamics and life history traits of a plant species may be influenced by a wide variety of phenomena acting at several different levels. Most population studies can be classified according to the phenomena and interactions considered (Solbrig 1980). Stated simply, these are 1.) energetic, 2.) genetical, and 3.) demographic. The energetic approach analyses the capture, transformation and allocation of energy to maintenance, growth and reproduction. Genetical analyses are concerned with the spatial and temporal variation of gene frequencies within populations and the influence of this variation upon fitness. The demographic approach is concerned with changes in the number of plant parts or numbers of individuals or classes of individuals through time. Unlike the other two methods, demographic studies do not rely upon destructive sampling. To obtain a comprehensive understanding of plant population dynamics and the action of natural selection, these three methods must be integrated; however, such an investigation would require long-term monitoring and manipulation of multiple populations both in a variety of habitats and under controlled conditions in the laboratory or greenhouse. Fortunately, particular aspects of population dynamics may be elucidated by the application of a single method. The demographic approach will be applied to a population of Cypripedium acaule in order to form hypotheses about the energetic restrictions to reproduction and the breeding system in this species.

The demography of many species of herbaceous perennial plants is complicated by a variety of traits. The only semipermanent plant parts may

occur underground, which increases the difficulty of identifying individuals. Clonal growth may be common (Bierzychudek 1982a). The unit designated as an individual must be defined, sometimes arbitrarily. The most common units are the genet (members of the same clone, whether connected to the parent or not) or the ramet (each unit of the clone that is capable of living independently). Ramets are often chosen as the unit of the population since it may not be possible to distinguish between parent and offspring without destructive sampling (e.g., Bierzychudek 1982b; Tamm 1972). Shoot position may vary slightly from year to year, making positive identification of genet members complicated (e.g., Tamm 1972, Wells 1967, Willems 1982). Unlike woody plants, herbaceous species may be difficult to age, although the root system may provide some indication of age, either through growth rings or the number of scales, buds, scars, or rootlets. Despite these problems, careful study has yielded information about the population dynamics of some forest perennials (e.g., Bierzychudek 1982b, 1984; Meagher and Antonovics 1982; Ashmun and Pitelka 1985; Pitelka et al. 1985). The study of orchid populations has an additional complication; obtaining estimates of reproductive success may be impossible in these species, especially those which are not conducive to greenhouse germination techniques. However, there have been a few long-term studies of orchid populations, including studies of 14 to 30 years duration on four European species (Tamm 1948, 1972), 15 years of observations on three grasslands orchid species (Wells 1967, 1981) and a 10 year study of the establishment of a population of the rare grasslands species Orchis simia (Willems 1982).

The Leslie matrix (Lewis 1942, Leslie 1945) and life table methods (Deevey 1947) ordinarily applied to animal populations are discrete time

models based on uniform age classes. The average fecundities of individuals in each age class and the probability of an individual of age t surviving to reach age $t+1$ may vary from age class to age class, but they are assumed to be constant through time. Given these fecundities and survival probabilities, it is possible to predict the eventual stable age distribution of the population under constant conditions and to determine if the population is growing or shrinking in size. The Leslie matrix has been successfully modified for the study of plants. The resulting model, known as the Lefkovitch matrix (Lefkovitch 1965), classifies individuals by some measure of size or life history stage instead of age (e.g., Harper 1967, Werner and Caswell 1977, Caswell and Werner 1978). The age class of an individual is always increasing, but increases in size may be reversible in plants. Thus the Lefkovitch model may have more nonzero entries than the Leslie matrix. Models of this type may be sensitive to the number of classes and their composition, so care must be taken when using size classes in order to minimize the influence of measurement errors and to avoid divisions which introduce artifactual errors due to the uneven distribution of individuals (Vandermeer 1978). In addition, the choice of time unit may also lead to inaccuracies which limit the predictive power of the model, particularly in species in which mortality is rare and episodic (e.g., Enright and Ogden 1979). Difficulties of this nature can be identified by testing the time invariance of the transition probabilities (Anderson and Goodman 1957).

The energetic importance of photosynthesis suggests one possible division of classes for life history analysis. Carbon fixation depends in part upon photosynthetic area. As a result, reproduction may be limited by leaf area. Unfortunately, in perennials the relationship between carbon fixation

and reproduction may be affected by the existence of storage organs which can be a source of energy captured in previous seasons. Also, mycorrhizal associates may possibly supply additional energy to some plant species; the relationship between leaf area and the amount of energy transferred is not known. However, rosette size (e.g., Werner and Caswell 1977), leaf number (e.g., Meagher 1982) and leaf area (e.g., Bierzychudek 1982b) still provide the most easily measured indicators of the energy available for perennation and reproduction. An alternative method is to consider reproductive state as an indicator of resource use and thus a predictor of future reproductive state (e.g., Bierzychudek 1984).

The demographic structure of a population of Cypripedium acaule was studied for four years. Both leaf number and leaf area will be used to describe the structure of this population. These data will be used to test the following hypotheses:

- H1. The reproductive state of a plant in year t is dependent upon leaf area in year t .
- H2. The reproductive state of a plant in year t is dependent upon leaf area in year $t-1$.
- H3. The dynamics of a population of C. acaule can be predicted from short-term data.

Materials and Methods.

All demographic data were collected on Clinch Mountain near Powder Spring Gap in Grainger County, Tennessee (USGS Lutrell Quadrangle). Three areas were sampled (Figure 2), all at about 500 to 600m elevation. Following a severe forest fire in the early 1950's which burned the entire

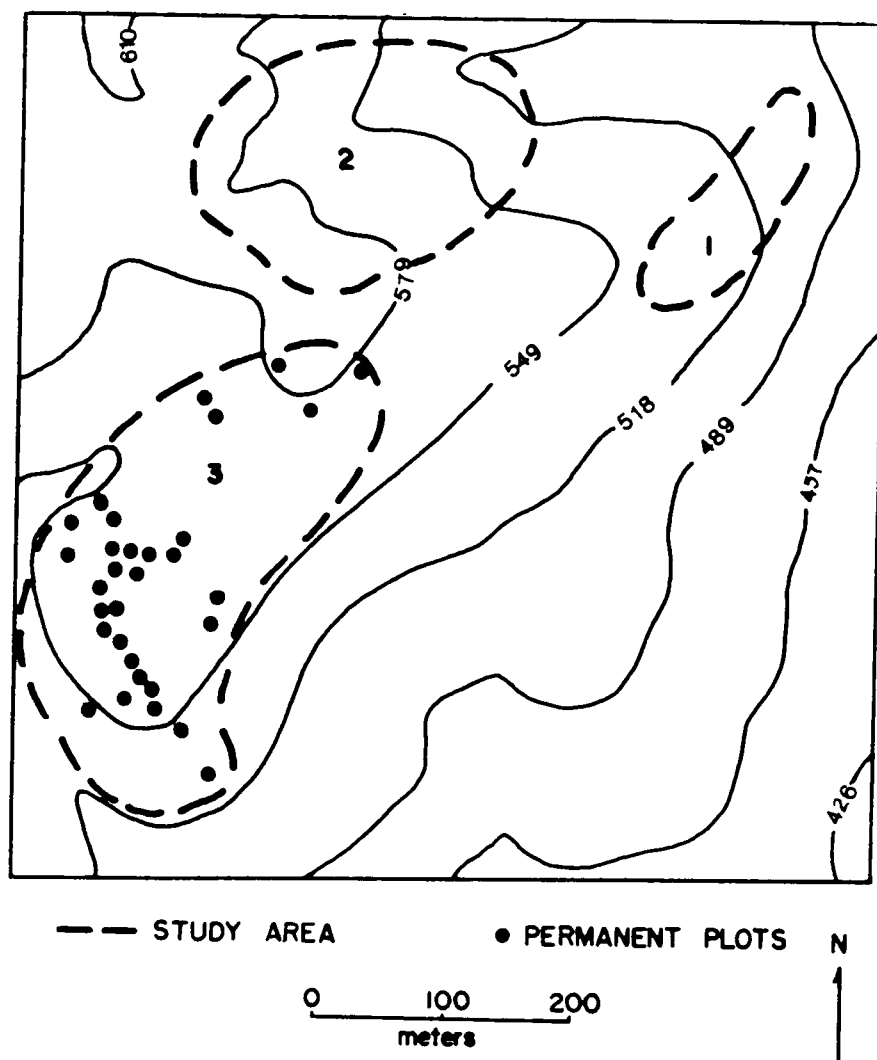


Figure 2: Locations of study patches on Clinch Mountain in Grainger County, Tennessee.

mountain range from Tennessee to Virginia, the study site was logged for commercial species. In addition, area 1 experienced a mild brush fire in the late 1960's. Area 2 was in light pasturage as recently as the late 1970's. Portions of area 3 were under cultivation or in pasturage prior to 1960. Three forest types occur: pine, chestnut oak and cove hardwood. Ericaceous shrubs occur throughout.

In 1984, 33 two-leaved plants in areas 2 and 3 were sampled for leaf area (Figure 3). Each leaf was measured, using a flexible clear plastic ruler, for width at the widest point and length from soil line to tip. Leaves were then removed at the soil line by cutting with an Exacto knife, placed in plastic bags and transported on ice. In the lab, twenty-five disks of radius 0.35 cm were cut from each leaf using a sharpened cork borer. The disks and the remainder of the leaf were dried in individual containers at 100°C for 24 hours, then weighed on a single pan balance to the nearest 0.001g. Whole leaf area was determined for each leaf by applying the relation between dry weight and area in the disks to whole leaf weight. Since destructive sampling is both undesirable and time consuming, a simple model of leaf area (measured length x width) was compared to leaf area by weight. Both model (length x width) and weight are subject to error. Thus, Model 1 regression is not appropriate for analysis (Sokal and Rohlf 1981). The correlation between the two measurements was calculated and several forms of Model 2 regression examined.

Permanent plots were established in area 3 in the following fashion. Locations containing C. acaule were chosen to represent a wide range of slope angles and exposures (Figure 4). All individuals with nearest- neighbor distances less than or equal to 1m were considered to be members of the

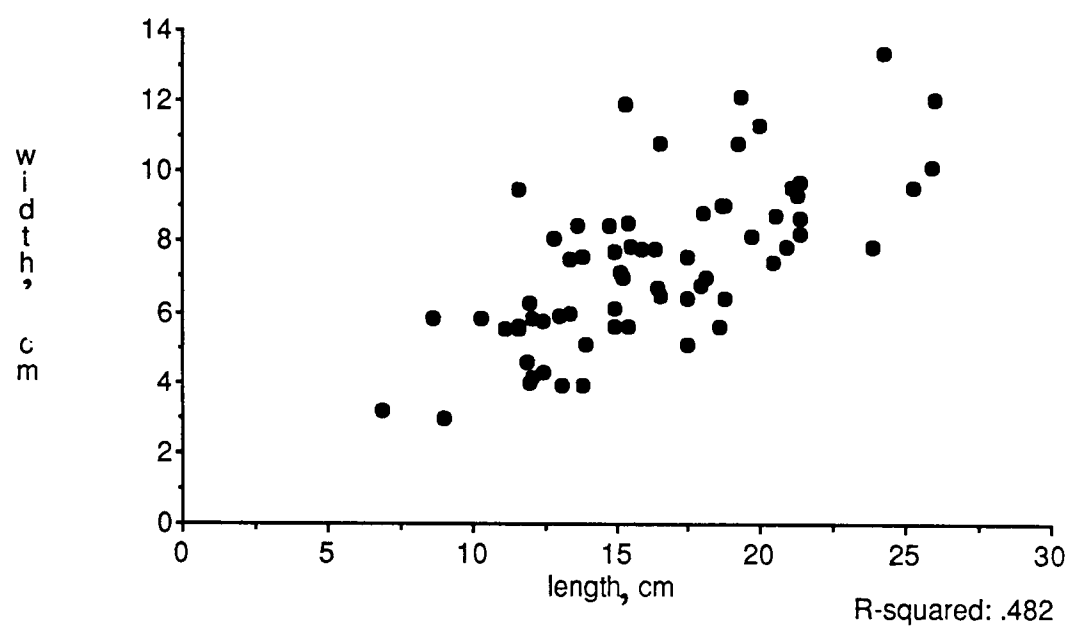


Figure 3: Distribution of leaf sizes used in leaf area determination.

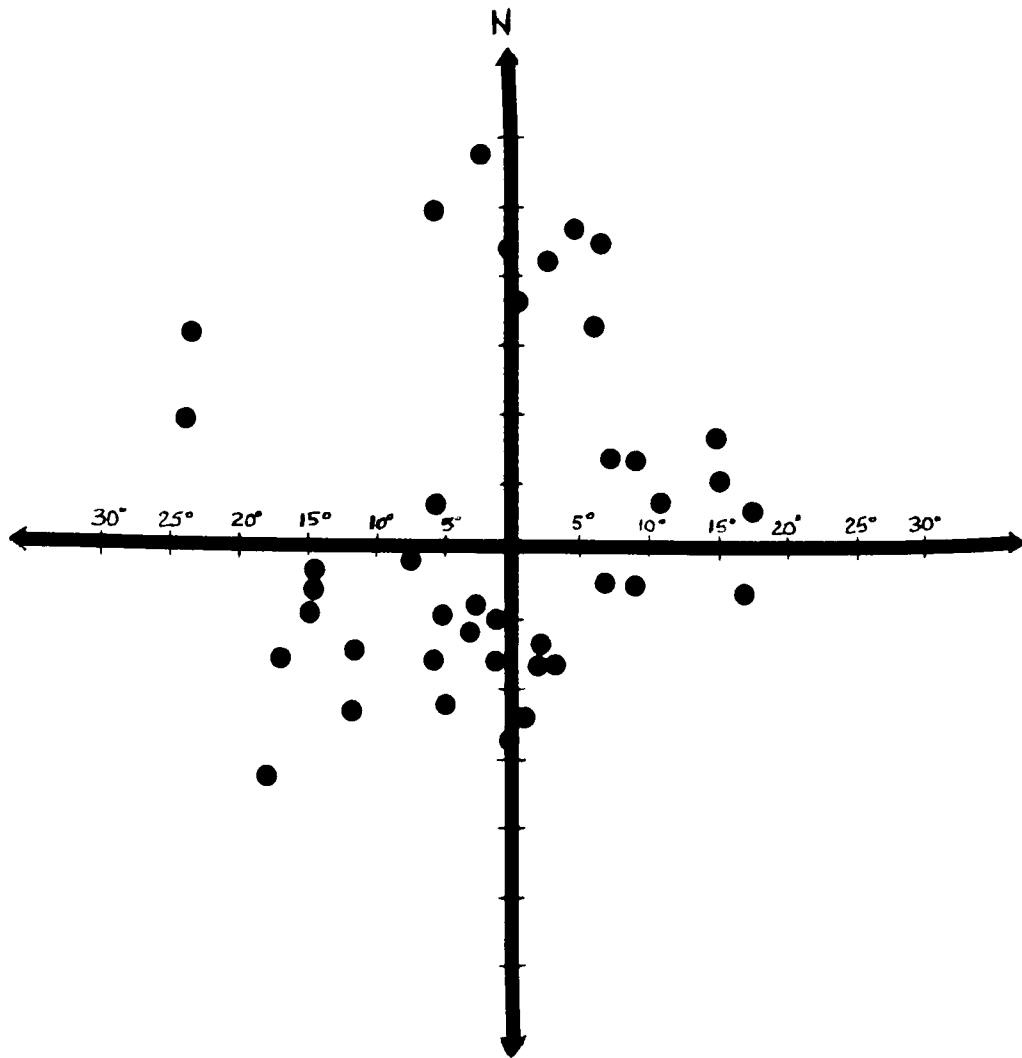


Figure 4: Polar distribution of patches by slope and aspect.

r = slope, a = aspect

same patch and were permanently tagged with plastic pot labels and assigned an identification number. An additional eleven temporary patches in area 2 were included in 1982 to complete the sampling of slope angles and exposures at this site.

During 1982-1985 a census of each patch was performed. The number of leaves, leaf dimensions, presence or absence of an inflorescence and presence or absence of fruit were recorded for each plant. Any identifiable cause of mortality (e.g. digging or burrowing by rodents) was recorded. Larger patches were mapped to the nearest 10cm.

As part of each census, all unmarked individuals were tagged. Despite thorough searching, a few tagged individuals were overlooked each season. Thirteen plants first tagged in 1982 but not counted in 1983 were recovered in the 1984 census, while eleven previously marked individuals not recorded in 1984 were sampled in 1985. In addition to these temporary omissions from the population, other circumstances resulted in the loss of tagged individuals from the sample. A total of 14 tags, presumably removed by humans, were recovered at another site. Six of these occurred in 1982 and the remainder in 1983. Intervention by animals (trampling, chewing of tags) and the upheaval of soil due to freezing resulted in an additional number of tags being removed from the vicinity of the plant. Four such tags were recovered in 1984 with an additional five found in 1985. The sampling method included all untagged plants as new recruits, but excluded absent individuals. All remaining lost tags were unaccounted for (see Table 1) and may be either omissions or removals. The maximum fraction of the sample for which data are unavailable in 1985 is 1.58%.

Table 1. Number of ramets not located in 1983-1985. Numbers in parentheses are tags recovered out of total number of missing plants.

Year	New ^a	Old ^b	Total lost ^c	Found ^d	Total tagged ^e
1983	28 (6)	0	28	0	1898
1984	38 (12)	15 (6)	53 (18)	13	2391
1985	45 (5)	42 (18)	87 (23)	11	2475

^a Tags first missing in year t.

^b Tags missing in previous years.

^c New + Old.

^d Tags missing in year t-1 but recorded in year t.

^e Tags assigned - tags recovered.

Transition probabilities (the probability of moving from size class *i* in year *a* to size class *j* in year *b*) were calculated for all individuals counted in both years *a* and *b*. Individuals for which there were no records (lost tags, temporary omissions and new recruits) were excluded from the computations, as were individuals whose death was established by the excavation of the rhizome following animal disturbances such as burrowing by rodents. One-year (1982-83, 1983-84, and 1984-85), two-year (1982-84 and 1983-85), and three-year (1982-85) transition matrices were calculated based on 1). number of leaves, 2). reproductive state (one-leaved, nonflowering two-leaved, flowering two-leaved or fruiting two-leaved), and 3). log transformed leaf area classes. Each set of transition matrices was tested for temporal constancy (Anderson and Goodman 1957) (i.e., the probability of moving from class *i* to class *j* is the same for each matrix in a set) and the Markov property (i.e., the two-year transitions are determined by the repeated application of the one-year transitions).

Results

Leaf area relationships. Values for the relationship between area by weight and the model length times width are shown in Figure 5. Length times width is highly positively correlated to area by weight ($r^2 = 0.9597$). Only 2% of the variance in leaf area by weight is unexplained by the model. Thus, for future discussion, leaf area will be assumed to be linearly related to length times width. In cases of high correlation, the various forms of linear regression (both Model 1 and Model 2) result in very similar equations (Sokal and Rohlf 1981). Model 1 regression results in the following relationship between length times width (A_{lw}) and area by weight (A_{wt}):

$$A_{wt} = 0.741 A_{lw} + 1.61$$

Patch composition. A total of 32 patches encompassing 1898 individuals were tagged in 1982. Patch sizes varied from six individuals to 430. The composition of these patches ranged from 100% flowering ramets to 100% nonflowering juveniles and is given in Table 2. Single factor analysis of variance (ANOVA, Sokal and Rohlf 1981) was performed on leaf area by patch for the following subclasses of ramets: one leafed, all two leaved, two leaved nonflowering and flowering, flowering but not setting fruit, and setting fruit (Table 3). The leaf area of each subgroup is significantly different between patches ($p < .005$) with the exception of fruiting ramets.

Size and stage distributions. Although there are a large number of small juveniles (Figure 6a), the size distribution of ramets changes gradually. Size classes were assigned by log transforming leaf area (i.e., Figure 6b), which provided reasonably uniform numbers in each class without apparent

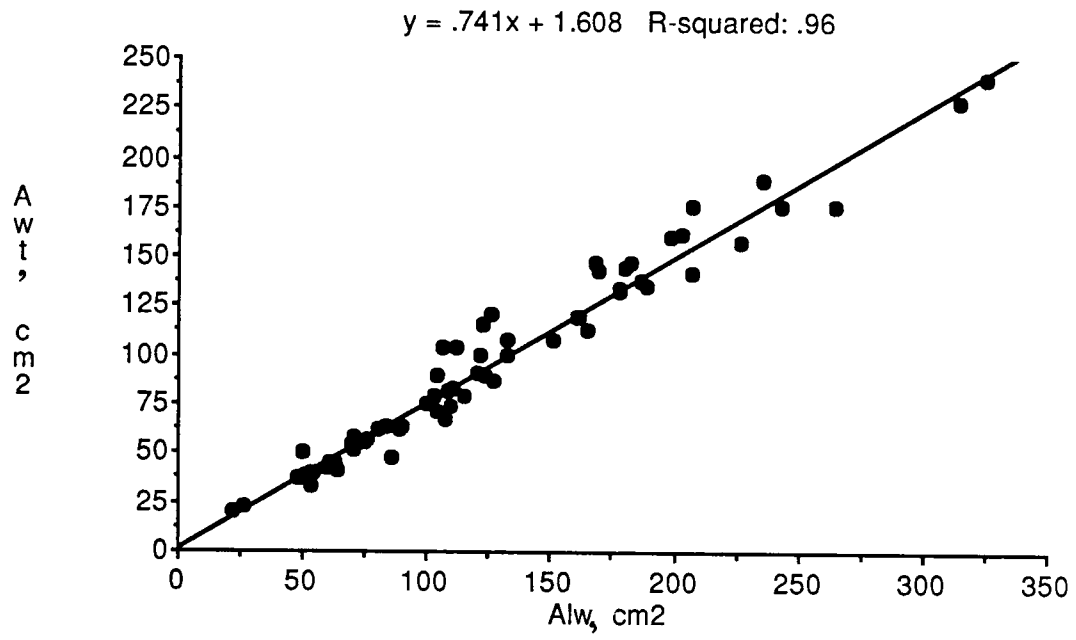


Figure 5: Leaf area model (A_{lw} = length x width) versus leaf area by weight (A_{wt}).

Table 2. Patch ramet composition by year and stage class. Percentages of total shoots given in parentheses for leaf classes, percentage of two-leaf shoots given for flowering shoots, and percentage of flowering shoots given for fruiting shoots.

Patch	Year	absent	1-leaf	2-leaf	Total	Flowering	Fruiting
1	1982	12 ^a (7.9)	79 (52.3)	60 (39.7)	151	25 [+2] ^b (41.7)	4 (16.0)
	1983	15 (7.9)	107 (56.6)	67 (35.4)	189	22 [+4] (32.8)	3 (13.6)
	1984	48 (24.4)	87 (44.2)	62 (31.5)	197	20 (32.3)	0
	1985	73 (36.3)	73 (36.3)	55 (27.4)	201	18 (32.7)	0
2	1982	0	0	26 (100.0)	26	18 (69.2)	2 (11.1)
	1983	16 (59.3)	0	11 (40.7)	27	6 [+2] (54.5)	2 (33.3)
	1984	2 (10.0)	1 (5.0)	17 (85.0)	20	4 (23.5)	0
	1985	2 (11.8)	0	15 (88.2)	17	9 (60.0)	1 (11.1)
3	1982	11 (8.7)	84 (66.1)	32 (25.2)	127	6 (18.8)	2 (33.3)
	1983	27 (15.2)	115 (64.4)	36 (20.2)	178	13 [+1] (36.1)	0
	1984	69 (38.1)	78 (43.1)	34 (18.8)	181	7 (20.6)	1 (14.3)
	1985	90 (45.5)	74 (37.4)	34 (17.2)	198	11 (32.4)	0
4	1982	1 (0.3)	120 (40.8)	173 (58.8)	294	82 (47.4)	20 (24.4)
	1983	48 (12.2)	189 (48.2)	155 (39.5)	392	41 [+30] (26.5)	5 (12.2)
	1984	109 (26.5)	141 (34.2)	162 (39.3)	412	29 (17.9)	0
	1985	147 (34.2)	120 (27.9)	163 (37.9)	430	47 [+1] (28.8)	6 (12.8)
5	1982	0	17 (17.0)	83 (83.0)	100	18 [+1] (18.8)	3 (16.7)
	1983	14 (12.2)	31 (27.0)	70 (60.9)	115	23 [+4] (32.9)	2 (8.7)
	1984	18 (15.3)	21 (17.8)	79 (66.9)	118	13 (16.5)	0
	1985	24 (20.0)	21 (17.5)	75 (62.5)	120	25 (33.3)	1 (4.0)

Table 2 (cont.)

Patch	Year	absent	1-leaf	2-leaf	Total	Flowering	Fruiting
6	1982	0	0	6 (100.0)	6	4 (66.7)	1 (25.0)
	1983	0	0	6 (100.0)	6	6 (100.0)	0
	1984	0	0	6 (100.0)	6	5 (83.3)	0
	1985	0	0	6 (100.0)	6	5 (83.3)	0
7	1982	0	11 (37.9)	18 (62.1)	29	7 [+1] (38.9)	1 (14.3)
	1983	0	14 (35.0)	26 (65.0)	40	9 [+2] (34.6)	2 (22.2)
	1984	2 (4.5)	13 (29.5)	29 (65.9)	44	11 (37.9)	1 (9.1)
	1985	5 (10.0)	16 (32.0)	29 (58.0)	50	10 (34.5)	3 (30.0)
8	1982	0	1 (8.3)	11 (91.7)	12	10 (90.9)	1 (10.0)
	1983	0	1 (7.1)	13 (92.9)	14	11 (84.6)	3 (27.3)
	1984	0	0	17 (100.0)	17	11 (64.7)	0
	1985	0	0	19 (100.0)	19	15 (78.9)	1 (6.7)
9	1982	0	1 (9.1)	10 (10.9)	11	8 (80.0)	4 (50.0)
	1983	0	9 (42.9)	12 (57.1)	21	11 [+1] (91.7)	1 (9.1)
	1984	7 (29.2)	4 (16.7)	13 (54.2)	24	9 (69.2)	2 (22.2)
	1985	4 (16.0)	5 (20.0)	16 (64.0)	25	12 (75.0)	1 (8.3)
10	1982	2 (1.5)	54 (40.9)	76 (57.6)	132	33 [+4] (43.4)	1 (3.0)
	1983	13 (8.3)	65 (41.4)	79 (50.3)	157	35 [+6] (44.3)	1 (2.9)
	1984	25 (14.8)	53 (31.4)	91 (53.8)	169	41 (45.1)	4 (9.8)
	1985	38 (21.6)	53 (30.1)	85 (48.3)	176	44 (51.8)	2 (4.5)

Table 2 (cont.)

Patch	Year	absent	1-leaf	2-leaf	Total	Flowering	Fruiting
11	1982	1 (2.4)	3 (7.1)	38 (90.5)	42	22 [+2] (57.9)	7 (31.8)
	1983	0	6 (12.2)	43 (87.8)	49	27 [+7] (62.8)	2 (7.4)
	1984	3 (5.3)	5 (8.8)	49 (86.0)	57	24 (49.0)	0
	1985	15 (26.8)	1 (1.8)	40 (71.4)	56	28 (70.0)	4 (14.3)
12	1982	0	17 (15.2)	95 (84.8)	112	65 [+1] (68.4)	17 (26.2)
	1983	5 (3.8)	20 (15.3)	106 (80.9)	127	77 [+5] (72.6)	5 (6.5)
	1984	16 (10.7)	13 (8.7)	120 (80.5)	149	68 (56.7)	1 (1.5)
	1985	23 (14.9)	11 (7.1)	120 (77.9)	153	83 (69.2)	6 (7.2)
13	1982	1 (0.5)	142 (75.1)	46 (24.3)	189	0	0
	1983	9 (3.4)	190 (72.0)	65 (24.6)	264	1 [+1] (1.5)	0
	1984	47 (17.0)	153 (55.2)	77 (27.8)	277	1 (1.3)	0
	1985	73 (25.3)	144 (49.8)	72 (24.9)	289	5 (6.9)	0
14	1982	0	0	8 (100.0)	8	4 [+1] (50.0)	2 (50.0)
	1983	0	0	8 (100.0)	8	8 (100.0)	2 (50.0)
	1984	1 (11.1)	0	8 (89.9)	9	4 (50.0)	0
	1985	1 (11.1)	0	8 (89.9)	9	5 (62.5)	0
15	1982	0	1 (7.1)	13 (92.9)	14	5 (38.5)	1 (20.0)
	1983	7 (50.0)	2 (14.3)	5 (35.7)	14	[+1]	0
	1984	0	2 (28.6)	5 (71.4)	7	3 (60.0)	0
	1985	0	2 (28.6)	5 (71.4)	7	4 (80.0)	0

Table 2 (cont.)

Patch	Year	absent	1-leaf	2-leaf	Total	Flowering	Fruiting
16	1982	0	0	12 (100.0)	12	10 [+1] (83.3)	5 (50.0)
	1983	1 (6.7)	0	14 (93.3)	15	8 [+1] (57.1)	1 (12.5)
	1984	2 (13.3)	2 (13.3)	11 (73.3)	15	7 (63.6)	0
	1985	2 (14.3)	0	12 (85.7)	14	10 (83.3)	0
17	1982	0	0	17 (100.0)	17	14 (82.4)	3 (21.4)
	1983	16 (94.1)	0	1 (5.9)	17	1 (100.0)	0
	1984	7 (50.0)	1 (7.1)	6 (42.9)	14	1 (16.7)	0
	1985	6 (46.2)	1 (7.7)	6 (46.2)	13	5 (83.3)	0
18	1982	0	5 (71.4)	2 (28.6)	7	0	0
	1983	0	8 (72.7)	3 (27.3)	11	0	0
	1984	1 (7.7)	9 (69.2)	3 (23.1)	13	0	0
	1985	2 (15.4)	8 (61.5)	3 (23.1)	13	0	0
19	1982	0	3 (18.8)	13 (81.3)	16	4 (30.8)	2 (50.0)
	1983	3 (16.7)	6 (33.3)	9 (50.0)	18	6 (66.7)	0
	1984	4 (18.2)	9 (40.9)	9 (40.9)	22	3 [+1] (33.3)	0
	1985	8 (34.8)	7 (30.4)	8 (34.8)	23	7 (87.5)	0
20	1982	0	25 (40.3)	37 (59.7)	62	9 (24.3)	3 (33.3)
	1983	6 (7.0)	30 (34.9)	50 (58.1)	86	20 (40.0)	0
	1984	28 (30.8)	18 (19.8)	45 (49.5)	91	3 (6.7)	0
	1985	23 (19.5)	46 (39.0)	49 (41.5)	118	9 (18.4)	0

Table 2 (cont.)

Patch	Year	absent	1-leaf	2-leaf	Total	Flowering	Fruiting
21	1982	0	2 (16.7)	10 (83.3)	12	5 (50.0)	1 (20.0)
	1983	2 (14.3)	2 (14.3)	10 (71.4)	14	7 (70.0)	2 (28.6)
	1984	0	4 (25.0)	12 (75.0)	16	5 (41.7)	0
	1985	2 (10.5)	3 (15.8)	14 (73.7)	19	8 (57.1)	1 (12.5)
22	1982	0	0	15 (100.0)	15	9 [+3] (60.0)	3 (33.3)
	1983	9 (56.3)	0	7 (43.7)	16	6 [+1] (85.7)	1 (16.7)
	1984	0	0	9 (100.0)	9	5 (55.6)	0
	1985	0	0	10 (100.0)	10	6 (60.0)	0
23	1982	0	129 (74.6)	44 (25.4)	173	5 [+2] (11.4)	1 (20.0)
	1983	51 (24.4)	123 (58.9)	35 (16.7)	209	7 (20.0)	0
	1984	117 (57.4)	60 (29.4)	27 (13.2)	214	2 (7.4)	0
	1985	132 (61.4)	55 (25.6)	28 (13.0)	215	3 (10.7)	0
24	1982	0	6 (14.6)	35 (85.4)	41	21 [+4] (60.0)	3 (14.3)
	1983	3 (5.5)	14 (25.5)	38 (69.0)	55	20 [+5] (52.6)	1 (5.0)
	1984	11 (19.3)	9 (15.8)	37 (64.9)	57	25 (67.6)	2 (8.0)
	1985	22 (37.9)	2 (3.4)	34 (58.6)	58	26 [+1] (76.5)	1 (3.8)
25	1982	0	7 (25.0)	21 (75.0)	28	7 [+2] (33.3)	1 (14.3)
	1983	3 (10.0)	6 (20.0)	21 (70.0)	30	13 [+2] (61.9)	0
	1984	3 (10.0)	7 (23.3)	20 (66.7)	30	11 [+1] (55.0)	1 (9.1)
	1985	6 (20.0)	5 (16.7)	19 (63.3)	30	8 (42.1)	0

Table 2 (cont.)

Patch	Year	absent	1-leaf	2-leaf	Total	Flowering	Fruiting
26	1982	0	0	9 (100.0)	9	1 [+1] (11.1)	0
	1983	1 (11.1)	0	8 (88.9)	9	2 [+1] (25.0)	0
	1984	0	3 (27.3)	8 (73.7)	11	0 [+1]	0
	1985	1 (9.1)	1 (9.1)	9 (81.8)	11	5 (55.6)	0
27	1982	0	1 (6.3)	15 (93.7)	16	12 (80.0)	3 (25.0)
	1983	2 (11.8)	0	15 (88.2)	17	8 [+3] (53.3)	0
	1984	0	1 (5.6)	17 (94.4)	18	10 (58.8)	0
	1985	2 (10.0)	1 (5.0)	17 (85.0)	20	11 (64.7)	0
28	1982	0	9 (22.5)	31 (77.5)	40	8 [+2] (25.8)	0
	1983	2 (4.0)	11 (22.0)	37 (74.0)	50	14 [+4] (37.8)	1 (7.1)
	1984	3 (5.5)	10 (18.2)	42 (76.4)	55	18 (42.9)	1 (5.6)
	1985	8 (13.3)	9 (15.0)	43 (71.7)	60	19 (44.2)	2 (10.5)
29	1982	0	13 (52.0)	12 (48.0)	25	5 [+1] (41.7)	1 (20.0)
	1983	3 (7.3)	20 (48.8)	18 (43.9)	41	4 [+2] (22.2)	1 (25.0)
	1984	10 (25.0)	11 (27.5)	19 (47.5)	40	5 (26.3)	0
	1985	16 (38.1)	10 (23.8)	16 (38.1)	42	3 (18.8)	0
30	1982	0	27 (48.2)	29 (51.8)	56	2 (6.9)	1 (50.0)
	1983	5 (7.5)	36 (53.7)	26 (38.8)	67	8 (30.8)	0
	1984	12 (17.9)	24 (35.8)	31 (46.3)	67	4 [+1] (12.9)	0
	1985	20 (29.0)	19 (27.5)	30 (43.5)	69	6 (20.0)	0

Table 2 (cont.)

Patch	Year	absent	1-leaf	2-leaf	Total	Flowering	Fruiting
31	1982	0	14 (42.4)	19 (57.6)	33	3 (15.8)	2 (66.7)
	1983	6 (15.0)	15 (37.5)	19 (47.5)	40	4 [+2] (21.1)	0
	1984	7 (15.9)	19 (43.2)	18 (40.9)	44	6 (33.3)	0
	1985	10 (23.3)	15 (34.9)	18 (41.9)	43	8 (44.4)	0
32	1982	0	13 (15.7)	70 (84.3)	83	18 [+1] (25.7)	6 (33.3)
	1983	4 (4.1)	25 (25.8)	68 (70.1)	97	22 [+5] (32.4)	2 (9.1)
	1984	7 (7.0)	22 (22.0)	71 (71.0)	100	23 (32.4)	1 (4.3)
	1985	18 (17.3)	15 (14.4)	71 (68.3)	104	25 (35.2)	2 (8.0)
Total	1982	28 (1.5)	784 (41.3)	1086 (57.2)	1898	440 [+49] (40.5)	101 (23.0)
	1983	271 (11.3)	1045 (43.6)	1071 (45.1)	2397	440 [+90] (40.7)	38 (8.6)
	1984	559 (22.4)	780 (31.3)	1154 (46.3)	2493	378 [+4] (32.8)	14 (3.7)
	1985	773 (29.5)	717 (27.4)	1129 (43.1)	2619	480 [+2] (42.5)	31 (6.5)

^a 1982 absent class present in early census but absent by canopy closure.

^b flowers killed in bud by frost and not available to pollinators.

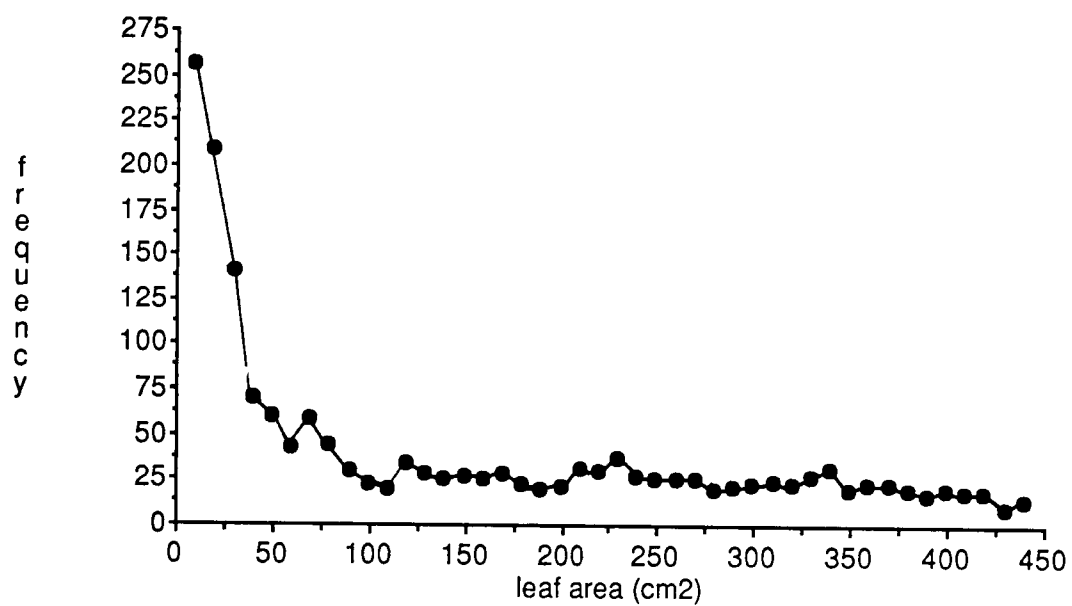
Table 3: Single classification analysis of variance (Sokal and Rohlf 1981) between patches for ramet leaf area by stage classification.

Class	Year	df/df ^a	FS	p
one-leafed	1982	24/759	4.040	< 0.001
	1983	23/1021	3.896	< 0.001
	1984	27/752	2.965	< 0.005
	1985	25/691	3.422	< 0.001
two-leaved	1982	31/1054	13.479	< 0.001
	1983	31/1049	15.550	< 0.001
	1984	31/1122	14.864	< 0.001
	1985	31/1097	15.239	< 0.001
nonflowering	1982	31/565	4.573	< 0.001
	1983	26/524	5.566	< 0.001
	1984	31/740	7.187	< 0.001
	1985	31/645	6.093	< 0.001
flowering	1982	29/410	4.079	< 0.001
	1983	29/410	4.843	< 0.001
	1984	29/348	4.238	< 0.001
	1985	30/449	4.823	< 0.001
not fruiting	1982	29/309	4.123	< 0.001
	1983	29/372	4.471	< 0.001
	1984	29/334	4.164	< 0.001
	1985	30/418	4.632	< 0.001
fruiting	1982	27/73	1.255	ns ^b
	1983	18/19	1.395	ns
	1984	8/5	1.211	ns
	1985	12/18	0.558	ns

^a degrees of freedom numerator/degrees of freedom denominator

^b not significant ($p > 0.05$)

a.



b.

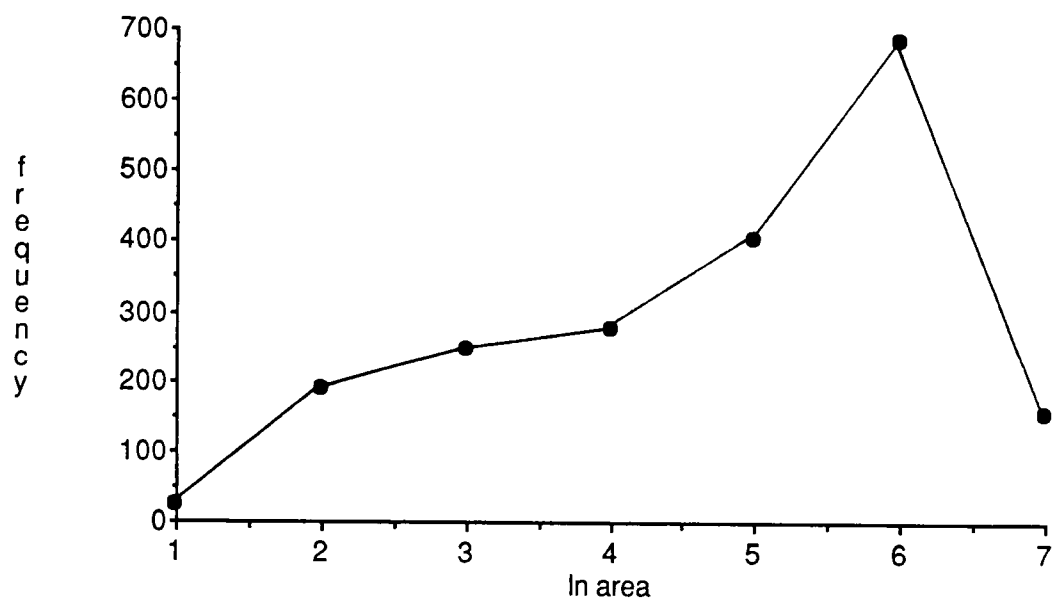


Figure 6: Leaf area distribution of ramets, 1985.

boundary effects; that is, size distributions based on log transformed leaf area of ramets did not change qualitatively after small changes in the criteria used to assign size classes. As total leaf area increases, ramets become more likely to produce two leaves (Figure 7). Small plants may alternate between bearing one and two leaves, but as plants age, they normally enter the two-leaved stage and remain there. The majority of ramets present in consecutive seasons remain the same size or increase in leaf area in the second year (Table 4); that is, for most ramets

$$A(t) - \Delta A(t) \leq A(t+1) + \Delta A(t+1),$$

where $A(t)$ is leaf area in year t , $\Delta A(t) = |\Delta w + w\Delta l|$ is the measurement error for area in year t , and Δw and Δl are the measurement errors for leaf width and length. Meteorological data are not available for this site; however, dry conditions in the spring of 1984 may explain the smaller leaf areas that year.

In some cases, individual genets consist of more than one ramet. In the larger genets, the number of shoots may vary from year to year. This may affect the analysis of ramet leaf area, since shoots present in one year and absent in the next were excluded from the previous discussion. However, a similar analysis of changes in leaf area based upon genets (Table 5) shows that, in general, the leaf area of genets also increases through time.

Flowering. Only a fraction of the mature ramets in the population flower in a particular year, approximately 40% of the two-leaved shoots present. This fraction usually represents less than 20% of the total number of ramets (Table 2, pp. 25-31). In addition, over the period 1982 to 1985, only 800 ramets, less than a third of the population during that period, produced

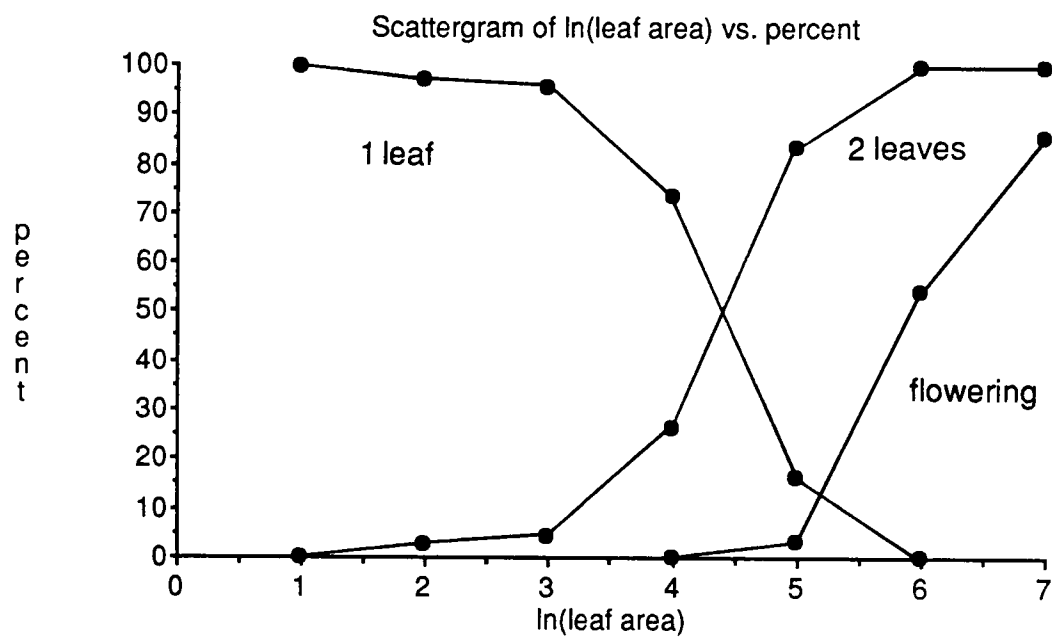


Figure 7: Ramet leaf area (cm^2) versus number of leaves 1985.

Table 4. Deviations in ramet leaf area greater than measurement error from year t to year $t+1$ ($A(t+1)-A(t)$) during 1982-1985 in a population of 2619 ramets.

years	# smaller ^a	# same ^b	#larger ^c	average change ^d	% larger or same
82-83	293	124	1173	31.85 cm ²	81.6
83-84	946	213	510	-13.98	43.3
84-85	405	247	963	22.63	74.9

^a $A(t+1) < A(t) - \Delta A(t) - \Delta A(t+1)$

^b $A(t) - \Delta A(t) - \Delta A(t+1) \leq A(t+1) \leq A(t) + \Delta A(t) + \Delta A(t+1)$

^c $A(t) + \Delta A(t) + \Delta A(t+1) < A(t+1)$

^d $A(t+1) - A(t)$

Table 5. Significant deviations in genet leaf area from year t to year $t+1$ ($A(t+1)-A(t)$). Classifications as in Table 4.

years	# smaller	# same	#larger	average change	% larger or same
82-83	239	114	1079	44.30	83.3
83-84	800	198	465	-9.33	45.3
84-85	363	208	820	22.95	73.9

flowers in one or more years. Most of these flowering ramets bloomed more than one year (Table 6).

Further reducing the number of potentially reproducing individuals is the fact that nearly half of the flowering ramets during this period were members of multi-shoot genets. In each year, over half of these multi-shoot genets produced more than one flower (Table 7).

Plant size is a good predictor of flowering state. Among the two-leaved ramets, those with the smallest leaf areas do not bloom. The probability that a ramet will flower increases with its leaf area in the current year (Table 8). As a result, the leaf area of flowering two-leaved ramets is significantly larger (one-tailed *t* test, $p=0.05$) than the leaf area of nonflowering two-leaved ramets (Table 9).

Flowering is also related to leaf area in the previous year. The probability that a ramet will flower in the following growing season increases with current leaf area (Table 10). In addition, flowering ramets had significantly larger leaf areas in the previous growing season than did nonflowering two-leaved ramets (Table 11).

Table 6. Total flower production by ramets during 1982-1985.

# years flowers produced	#ramets	% of all flowering ramets
1	249	31.1
2	196	24.5
3	179	22.4
4	176	22.0
Total	800	100.0

Table 7. Annual flower production by genets during 1982-1985. Tabulated values are the number of genets in each category.

plant type	1982	1983	1984	1985	Total
#single shoot genets with 1 flower	258	243	163	228	892
#multiple shoot genets with:					
1 flower	36	42	58	48	184
2 flowers	36	42	43	56	177
3 flowers	10	14	14	18	56
4 flowers	6	2	2	4	14
5 flowers	4	3	3	3	13
6 flowers	0	1	1	0	2
7 flowers	0	0	0	1	1
Total flowering genets	350	347	284	358	1339
% genets flowering	22.1	18.2	16.8	22.3	19.7
Total # flowers	440	440	378	480	1738
#flowers from multi-shoot genets	182	197	215	252	846

Table 8. Frequency of flowering for ramet size classes based upon $\ln(A(t))$, where $A(t)$ is leaf area (cm^2) in year t .

year	$-\infty < \ln(A) \leq 3$	$3 < \ln(A) \leq 4$	$4 < \ln(A) \leq 5$	$5 < \ln(A) \leq 6$	$6 < \ln(A) \leq 7$
1983	0.000	0.0142	0.0671	0.651	0.932
1984	0.000	0.0037	0.0374	0.446	0.821
1985	0.000	0.000	0.0385	0.540	0.860

Table 9. Comparison of mean leaf area, $A(t)$, in cm^2 of flowering ramets versus mean leaf area of nonflowering ramets. One-tailed t-test of the hypothesis that flowering ramets have a larger mean area.

year	type	n	A	s	t	p
1982	flowering	489	298.1	118.4	26.5	< 0.025
	nonflowering	597	130.6	89.5		
1983	flowering	530	338.3	128.1	28.0	< 0.025
	nonflowering	551	141.2	102.0		
1984	flowering	382	325.0	106.7	18.9	< 0.025
	nonflowering	772	156.6	156.6		
1985	flowering	482	348.9	125.5	26.7	< 0.025
	nonflowering	647	163.3	107.7		

Table 10. Frequency of flowering in year t for ramet size classes based upon $\ln(A(t-1))$, where $A(t-1)$ is leaf area (cm^2) in the previous year.

year	$-\infty < \ln(A) \leq 3$	$3 < \ln(A) \leq 4$	$4 < \ln(A) \leq 5$	$5 < \ln(A) \leq 6$	$6 < \ln(A) \leq 7$
1983	0.000	0.0107	0.168	0.750	0.781
1984	0.0023	0.0029	0.0225	0.448	0.760
1985	0.000	0.0038	0.0470	0.572	0.874

Table 11. Comparison of mean leaf area (cm^2) in year $t-1$ of ramets flowering in year t versus mean leaf area in year $t-1$ of ramets not flowering in year t . One-tailed t -test of the hypothesis that flowering ramets have a larger mean area.

year	type	n	A	s	t	p
1983	flowering	458	272.1	111.0	11.4	< 0.025
	nonflowering	488	110.7	101.7		
1984	flowering	362	358.7	132.4	13.5	< 0.025
	nonflowering	701	149.2	124.2		
1985	flowering	445	308.7	107.0	10.4	< 0.025
	nonflowering	606	133.2	97.2		

Dormancy. Dormancy (i.e., producing no above ground parts through one or more growing seasons) has been suggested as a mechanism by which herbaceous perennials can avoid adverse conditions. Dormancy occurs in many orchid species but does not appear to be common among mature individuals in this population of *C. acaule*. Of 108 ramets absent one year but present in the previous and following years, only 27 were ever observed to flower. The entire genet was absent in only two of these cases. This represents about 0.2% of the flowering genets. Dormancy is more common among one-leafed genets. Of 784 juveniles present in 1982 and 1984, 16 (approximately 2%) were dormant in 1983. Juvenile dormancy over the period 1983-1985 was about half as common as that in 1982-1984.

Recruitment and mortality. The recruitment of new individuals into the population is summarized in Table 12. Two aspects of the population dynamics make 1983 an extraordinary season. First, the recruitment of juveniles (one-leafed individuals) was high. Secondly, adult mortality was high due to the complete destruction of the above ground parts of 103 adults

Table 12: Stage distribution of recruits, 1983-1985.

Year	1-leafed	2-leaved ^a	3-leaved	flowering ^b	fruiting ^c	total	% ^d
1983	432	60	0	34	0	526	21.9
1984	102	58	1	5	0	166	6.7
1985	120	34	0	5	1	160	6.1
Total	634	152	1	44	1	852	

^a 2 leaves, nonflowering

^b 2 leaves, flowering, not fruiting

^c 2 leaves, flowering, fruiting

^d % of total population that year

by rodents. Of these, 53 suffered sufficient rhizome damage to kill the plant (Table 13). Among the survivors, most exhibited reduced leaf area in 1984 but returned to near normal size and collectively produced 14 flowers in 1985.

Annual estimates of mortality are given by the number of ramets absent in year *t* and all subsequent years (Table 13). Based on this estimation, shoot recruitment only slightly exceeded shoot mortality (853 new recruits versus 805 deaths). In particular, 85.5% of the 1984 recruit class failed to reappear in 1985.

Stage transitions. Since information about the fecundity of the pink lady's-slipper is not readily available, it is not possible to use a Lefkovitch

Table 13: Estimate of percent ramet mortality by stage class (percentage of stage class in previous year).

year	recruits ^a	one-leaved ^b	two-leaved	flowering	fruiting	total	population
1983 ^c		9.3 [73] ^d 1.4 [11]	3.2 [19] 3.0 [18]	0.8 [3] 4.9 [19]	0.0 [0] 5.0 [5]	5.0 [95] 2.8 [53]	[1898]
1984	32.5 [171]	24.1 [148]	3.5 [17]	0.4 [2]	7.9 [3]	14.2 [341]	[2397]
1985	85.5 [142]	16.1 [109]	3.9 [30]	6.9 [25]	64.3 [9]	12.6 [315]	[2493]
Total	[313]	[341]	[85]	[49]	[17]	[804]	

^a First appeared in the previous year.

^b Remaining classifications as in Table 12.

^c Second row of entries for 1983 is shoots eaten by rodents.

^d Sample size

model to predict population dynamics. However, a transition probability matrix of the Lefkovitch type can be used to predict the eventual stage distribution of the individuals present at any given time, provided that the transition probabilities are constant through time and satisfy the Markov property. Number of leaves provides a simple size class structure for modeling the dynamics of ramets. However, this classification fails to satisfy both assumptions. First, one year transition probabilities (Table 14) are not constant through time ($X^2 = 216.48$, $df = 24$, $p < 0.001$; Anderson and Goodman 1957). Secondly, the transitions do not satisfy the Markov property (i.e., the probability of moving from state i in year t to state j in year $t+2$ (Table 15) or the probability of moving from state i in year t to state j in year $t+3$ (Table 16) cannot be determined from the one year transition probabilities). The greatest deviation from the constancy assumption comes in the 0 ($X^2 = 90.87$, $df = 6$, $p < 0.001$) and 1 leaf size classes ($X^2 = 11.73$, $df = 6$, $p < 0.001$), largely due to unpredictable changes in the rates of juvenile mortality from year to year. The stable stage distributions, found by iterating each matrix, are also qualitatively different from each other (Table 17). In particular, iterating the 1984-1985 transition matrix predicts a decline in the number of two-leaved ramets compared to the 1982-1983 and 1983-1984 predictions. The observed distribution, found by averaging the population distribution over the years 1983-1985, is intermediate to the predicted values (Table 17).

Lumping the small number of three-leaved individuals with the two-leaved shoots has no influence on the level of constancy ($X^2 = 212.08$, $df = 4$, $p < 0.001$). A further refinement of the stage classification model which subdivides the two-leaved class into flowering and non-flowering ramets

Table 14: One year transition probabilities for ramets based on leaf number. Column sample size given in brackets.

		1982			
		0 ^a	1	2	3
1983	0 ^b	0.667	0.132	0.054	0.000
	1	0.267	0.738	0.042	0.000
	2	0.067	0.130	0.899	1.000
	3	0.000	0.000	0.003	0.000
		[15] ^c	[684]	[922]	[3]
		1983			
		0	1	2	3
1984	0	0.568	0.345	0.069	0.000
	1	0.167	0.557	0.058	0.000
	2	0.252	0.098	0.867	1.000
	3	0.014	0.000	0.006	0.000
		[222]	[938]	[1060]	[3]
		1984			
		0	1	2	3
1985	0	0.869	0.275	0.079	0.000
	1	0.075	0.627	0.059	0.000
	2	0.050	0.098	0.860	0.900
	3	0.006	0.000	0.002	0.100
		[518]	[706]	[1128]	[10]

^a leaf number in year t^b leaf number in year t+1^c sample size

Table 15: Two-year transitions for ramets based on leaf number^a.

		1982			
		0	1	2	3
1984	0	0.706	0.331	0.091	1.000
	1	0.118	0.499	0.069	0.000
	2	0.176	0.171	0.831	0.000
	3	0.000	0.000	0.009	0.000
		[17]	[708]	[1028]	[2]

		1983			
		0	1	2	3
1985	0	0.595	0.466	0.106	0.333
	1	0.107	0.431	0.074	0.000
	2	0.293	0.103	0.815	0.667
	3	0.005	0.000	0.005	0.000
		[215]	[929]	[1053]	[3]

^a transitions from year t to year $t+2$. Entries as in Table 14.

Table 16: Three year transition for ramets based on leaf number^a

		1982			
		0	1	2	3
1985	0	0.800	0.438	0.125	0.500
	1	0.050	0.409	0.068	0.000
	2	0.150	0.154	0.802	0.500
	3	0.000	0.000	0.006	0.000
		[20]	[697]	[1018]	[2]

^a Transitions from year t to year $t+3$. Entries as in Table 14.

Table 17. Comparison of observed stage distribution with the stable stage distributions (expressed as percentage of total population) associated with ramet leaf number transition matrices.

	leaf area class	percent of total
average observed stage distribution	0	0.214
	1	0.339
	2	0.445
	3	0.002
stable stage distribution for 1982-1983	0	0.194
	1	0.281
	2	0.510
	3	0.002
stable stage distribution for 1983-1984	0	0.231
	1	0.165
	2	0.598
	3	0.007
stable stage distribution for 1984-1985	0	0.519
	1	0.156
	2	0.321
	3	0.004

(Table 18) is no more successful than the leaf number classification in satisfying the assumptions of the model ($X^2 = 312.08$, $df = 60$, $p < 0.001$).

Leaf area transitions. Since classification by leaf number and flowering status failed to satisfy the assumptions of the Lefkovitch model, the population was divided into size classes based upon log transformed leaf area. However, the probability of moving from one size class to another (Table 19) is even more variable through time than the transition probabilities based on leaf number ($X^2 = 812.08$, $df = 112$, $p < 0.001$). Thus, the transition probability model based on four years of data is inappropriate for modeling C. acaule population dynamics.

Size/stage transition probabilities. Similar transition probabilities may be computed to determine whether leaf area in year $t-1$ influences vegetative or flowering state in year t (Table 20). Once again, these transition probabilities are not constant through time ($X^2 = 1677.5$, $df = 80$, $p < 0.001$), but they do reveal strong relationships between leaf area in year $t-1$ and the probability of flowering or the probability of being absent in year t . The largest size class (length $\times$ width ≥ 1096.6 cm²) does satisfy the constancy condition ($X^2 = 11.28$, $df = 10$, $p > 0.05$), indicating that once shoots reach a certain size, they have a consistently high probability of flowering (75-87%). Leaf area in year t is a more reliable predictor of stage in year t than is leaf area in year $t-1$. Vegetative and flowering state in year $t-1$ is not as strongly related to leaf area in year t (Table 21). Only the fruiting class has constant transition probabilities ($X^2 = 1.80$, $df = 14$, $p > 0.05$). However, stage in year $t-1$ is a slightly better predictor of leaf area in year t than stage in year t is.

Table 18: Transition probabilities for ramets based on leaf number and flowering state. Column sample size given in parentheses.

1982-1983					
leaf number	0 ^a	1	2	3	Fl
0	0.680	0.124	0.073	0.000	0.030
1	0.160	0.748	0.073	0.000	0.005
2	0.160	0.124	0.580	0.500	0.167
3	0.000	0.000	0.002	0.000	0.005
Fl	0.000	0.004	0.272	0.500	0.794
	[25]	[758]	[547]	[2]	[432]
1983-1984					
leaf number	0	1	2	3	Fl
0	0.580	0.343	0.073	0.000	0.064
1	0.165	0.563	0.105	0.000	0.018
2	0.234	0.094	0.699	0.333	0.314
3	0.013	0.000	0.007	0.000	0.005
Fl	0.009	0.000	0.116	0.667	0.600
	[231]	[1018]	[545]	[3]	[440]
1984-1985					
leaf number	0	1	2	3	Fl
0	0.872	0.269	0.095	0.000	0.053
1	0.075	0.639	0.087	0.000	0.008
2	0.040	0.087	0.583	0.500	0.189
3	0.006	0.000	0.003	0.100	0.000
Fl	0.007	0.005	0.233	0.400	0.750
	[546]	[762]	[760]	[10]	[376]

^a 0, 1, 2, 3 - number of leaves in nonflowering ramets; Fl - flowering ramets

Table 19: One-year transition probabilities for ramets based on leaf length x width (cm^2). Entry a_{ji} = (probability of ramet size i in year t becoming size j in year $t+1$). Size class $-\infty$ consists of those ramets with 0 leaf area. Category n represents ramets with $n-1 < \ln(\text{leaf area } (\text{cm}^2)) \leq n$. Column sample sizes given in brackets.

1982-1983								
$\ln(\text{leaf area})$	$-\infty$	1	2	3	4	5	6	7
$-\infty$	0.680	0.354	0.169	0.084	0.085	0.063	0.043	0.037
1	0.040	0.231	0.076	0.000	0.000	0.000	0.000	0.000
2	0.040	0.292	0.234	0.111	0.004	0.011	0.002	0.000
3	0.120	0.108	0.429	0.411	0.075	0.011	0.006	0.024
4	0.000	0.015	0.087	0.333	0.413	0.031	0.024	0.037
5	0.080	0.000	0.005	0.060	0.399	0.455	0.047	0.037
6	0.040	0.000	0.000	0.000	0.021	0.431	0.691	0.220
7	0.000	0.000	0.000	0.000	0.004	0.000	0.187	0.646
	[25]	[65]	[194]	[333]	[281]	[289]	[508]	[82]
1983-1984								
$\ln(\text{leaf area})$	$-\infty$	1	2	3	4	5	6	7
$-\infty$	0.591	0.934	0.529	0.290	0.137	0.137	0.090	0.038
1	0.018	0.033	0.145	0.030	0.006	0.003	0.000	0.000
2	0.032	0.033	0.215	0.228	0.029	0.000	0.002	0.000
3	0.041	0.00	0.095	0.362	0.269	0.019	0.007	0.006
4	0.059	0.000	0.008	0.069	0.409	0.151	0.013	0.000
5	0.136	0.000	0.004	0.009	0.111	0.576	0.090	0.006
6	0.118	0.000	0.004	0.012	0.038	0.161	0.796	0.472
7	0.005	0.000	0.000	0.000	0.000	0.000	0.031	0.478
	[220]	[61]	[242]	[434]	[432]	[311]	[545]	[159]
1984-1985								
$\ln(\text{leaf area})$	$-\infty$	1	2	3	4	5	6	7
$-\infty$	0.879	0.635	0.390	0.227	0.091	0.097	0.075	0.021
1	0.013	0.175	0.065	0.012	0.000	0.000	0.000	0.011
2	0.021	0.143	0.335	0.093	0.015	0.00	0.000	0.000
3	0.028	0.048	0.170	0.441	0.088	0.009	0.002	0.000
4	0.021	0.000	0.040	0.202	0.532	0.053	0.006	0.000
5	0.017	0.000	0.000	0.022	0.255	0.580	0.048	0.000
6	0.021	0.000	0.000	0.003	0.019	0.260	0.751	0.147
7	0.002	0.000	0.000	0.000	0.000	0.000	0.119	0.821
	[535]	[63]	[267]	[322]	[263]	[319]	[650]	[95]

Table 20: Ramet transition probabilities from leaf area (cm^2) in year $t-1$ to stage in year t .
 Entry a_{ij} = (probability of ramet size i in year $t-1$ being stage j in year t). Size classes as in Table 18. Stage classes: 0 - no leaves; 1 - 1 leaved; 2 - 2-leaved, nonflowering; 3 - 3-leaved, nonflowering; Fl - 2-leaved, flowering, nonfruiting; and Fr - fruiting. Column sample sizes given in brackets.

1982								
ln(leaf area)	$-\infty$	1	2	3	4	5	6	7
1983 stage								
0	0.680	0.354	0.169	0.084	0.085	0.063	0.041	0.024
1	0.160	0.631	0.799	0.808	0.484	0.046	0.004	0.012
2	0.160	0.015	0.033	0.108	0.420	0.724	0.199	0.183
3	0.000	0.000	0.000	0.000	0.000	0.000	0.006	0.000
Fl	0.000	0.000	0.000	0.000	0.011	0.154	0.695	0.055
Fr	0.000	0.000	0.000	0.000	0.000	0.014	0.055	0.073
	[25]	[65]	[182]	[297]	[281]	[286]	[508]	[82]
1983								
ln(leaf area)	$-\infty$	1	2	3	4	5	6	7
1984 stage								
0	0.591	0.934	0.529	0.290	0.137	0.090	0.061	0.038
1	0.155	0.066	0.463	0.661	0.567	0.087	0.024	0.013
2	0.232	0.000	0.008	0.046	0.292	0.797	0.459	0.189
3	0.014	0.000	0.000	0.00	0.000	0.003	0.009	0.000
Fl	0.009	0.000	0.000	0.002	0.003	0.023	0.426	0.748
Fr	0.000	0.000	0.000	0.000	0.000	0.000	0.022	0.013
	[220]	[61]	[242]	[434]	[342]	[311]	[545]	[159]
1984								
ln(leaf area)	$-\infty$	1	2	3	4	5	6	7
1985 stage								
0	0.879	0.635	0.390	0.227	0.091	0.097	0.075	0.021
1	0.069	0.365	0.600	0.724	0.563	0.082	0.008	0.011
2	0.039	0.000	0.010	0.050	0.342	0.771	0.342	0.095
3	0.006	0.000	0.000	0.000	0.000	0.003	0.003	0.000
Fl	0.008	0.000	0.000	0.000	0.004	0.044	0.535	0.821
Fr	0.000	0.000	0.000	0.000	0.000	0.003	0.037	0.053
	[535]	[63]	[200]	[322]	[254]	[319]	[650]	[95]

Table 21: Ramet transition probabilities from stage in year t-1 to leaf area in year t.
 Entry a_{ji} = (probability of ramet stage i in year t-1 being size j in year t).
 Size and stage classes as in Table 19. Column totals given in brackets.

1982 stage	0	1	2	3	Fl	Fr
1983 ln(leaf area)						
∞	0.680	0.140	0.135	0.000	0.143	0.129
1	0.040	0.038	0.000	0.000	0.000	0.000
2	0.040	0.127	0.009	0.000	0.003	0.000
3	0.120	0.302	0.024	0.000	0.008	0.020
4	0.000	0.266	0.087	0.000	0.029	0.010
5	0.080	0.122	0.292	0.500	0.049	0.050
6	0.040	0.007	0.410	0.500	0.525	0.495
7	0.000	0.000	0.043	0.000	0.244	0.297
	[25]	[772]	[585]	[2]	[385]	[103]
1983 stage	0	1	2	3	Fl	Fr
1984 ln(leaf area)						
∞	0.725	0.343	0.073	0.000	0.065	0.105
1	0.019	0.048	0.007	0.000	0.000	0.000
2	0.031	0.156	0.007	0.000	0.002	0.000
3	0.038	0.244	0.059	0.000	0.006	0.000
4	0.050	0.147	0.128	0.000	0.014	0.000
5	0.088	0.056	0.345	0.333	0.049	0.053
6	0.044	0.006	0.365	0.667	0.707	0.632
7	0.006	0.000	0.015	0.000	0.157	0.211
	[160]	[772]	[1018]	[3]	[492]	[38]
1984 stage	0	1	2	3	Fl	Fr
1985 ln(leaf area)						
∞	0.879	0.269	0.095	0.000	0.049	0.143
1	0.013	0.035	0.001	0.000	0.003	0.000
2	0.021	0.139	0.005	0.000	0.000	0.000
3	0.028	0.244	0.024	0.000	0.006	0.000
4	0.021	0.222	0.084	0.000	0.003	0.000
5	0.017	0.074	0.291	0.100	0.030	0.071
6	0.021	0.017	0.447	0.900	0.604	0.571
7	0.002	0.000	0.053	0.000	0.306	0.214
	[535]	[762]	[760]	[10]	[366]	[14]

Discussion

A number of factors influence reproduction, recruitment and mortality in the pink lady's slipper. A small proportion of individuals flower and of these, an even smaller proportion actually succeeds in setting seed. Episodic recruitment may indicate that new recruits are the product of a single successful pollination. Seed production varies significantly through time, or environmental factors important to germination and establishment (including, perhaps, factors influencing the mycorrhizal associate) may fluctuate to such an extent that recruitment is reduced in some years. The juvenile stages of perennial plants usually are the most vulnerable to environmental fluctuations, especially water stress, since they have not yet developed sufficient storage organs, so widely varying rates of juvenile mortality are not surprising. However, the loss of adults from the population through predation on the rhizomes (or due to poaching) can have a significant impact on the population. New recruits are slow to replace adults; only one individual advanced from the one leaf class in 1982 to the flowering class in 1985.

Since recruitment and mortality in this species are unpredictable, there are not sufficient data to make quantitative predictions about the population structure in the future. However, the following qualitative observations are possible:

1. Both ramets and genets generally maintain or increase their leaf area from year to year.
2. Only a small fraction of either the mature ramets or mature genets in a population flower in a particular year.
3. The smallest plants do not flower and the probability that a ramet will flower in a given year increases with its leaf area in that year.

4. The probability that a ramet will flower is very closely related to its leaf area in the previous year.
5. Juveniles may fail to appear above ground in some years without dying. Adults are seldom dormant.
6. Juvenile mortality is high and the juvenile class fluctuates from year to year.
7. Adults do not appear to senesce. Adult mortality is low and usually is caused by interactions with herbivores.

In general, plants maintain their size and flowering status; the best predictor of future size or stage is present size or stage. However, it is not clear whether demographic data over a longer time period could allow quantitative predictions or if the population under consideration is controlled by stochastic events such as weather which would make such predictions difficult.

CHAPTER 4

POLLINATION ECOLOGY

Resource and pollen availability, acting independently or together, may limit long-term reproductive success in plant species (i.e., the number of offspring produced during an individual's life span). Resource limitation usually is chosen as the null hypothesis and most research has focused on its short-term effects (i.e., the reduction of flower, fruit or seed production in a single growing season; for a review, see Rathke 1983, Willson and Burley 1983). In plants which exhibit both short-term pollen limitation and short-term resource limitation, the relative strength of the two effects must be assessed in order to determine which factor limits long-term reproductive success. If repeated successful pollination results in resource limitation of flower production, fruit set or seed set or in increased mortality, the total fitness of an individual may be decreased (Janzen et al 1980). Generally it is accepted that in order to demonstrate pollen limitation, hand pollinated individuals must have higher long-term reproductive success than naturally pollinated ones (e.g., Janzen et al. 1980, Bierzychudek 1981, Willson and Burley 1983, although, see Hainsworth et al 1985). Short-term resource limitation may be shown by constant fruit or seed set under increased pollination, increased fruit or seed set following the application of fertilizer, decreased fruit or seed set following defoliation, or decreased flower, fruit or seed production following fruit set, either in the same growing season or in subsequent years (Willson and Burley 1983).

Pollen limitation may occur in three ways. First, there may be an imbalance in sexual allocation to male function. In other words, despite an

adequate number of efficient pollen vectors, there is insufficient pollen to fertilize all ovules. In this case, the pollen itself is truly limiting reproductive success. Secondly, pollen vectors may be inefficient, either eating pollen (e.g., Heinrich 1976a), transferring mixed species pollen loads that cause interference on the stigma (e.g., Campbell 1985, Campbell and Motten 1985), or simply failing to deliver pollen to the stigma during a visit to a flower (e.g., Bierzychudek 1981, Snow 1982). Under these circumstances, the apparent pollen supply is limiting. Selection would be expected to act on traits which increase pollinator fidelity or efficiency rather than on allocation of energy to male function. Finally, if most flowers are never visited by a pollinator, it is this visitation level that is limiting reproductive success. In this situation, often described as pollinator limitation, selective pressure should be strong on traits that influence the attraction of pollinators. Just as a plant may experience both pollen and resource limitation, more than one of these cases may occur in the same species; however, it is expected that one force will predominate.

The foraging behavior of some pollinators has been investigated. Much research has focused on the foraging behavior of the bumblebees (Bombus). Each bee forages individually without communicating with other members of the hive. Initially, a bee samples the available flowers, then specializes on a limited number of the most rewarding species (Heinrich 1976a, 1979b). In particular, bumblebees quickly learn to avoid species which never offer a reward. The honeycrop of a bumblebee can hold up to 0.2ml of nectar before it must return to the hive. Bumblebees are capable of thermoregulation and can forage profitably at temperatures as low as 3°C by reducing the amount of energy-consuming flying in favor of walking and by

taking advantage of solar radiation and the thermal protection (e.g., protection from wind, orientation towards the sun, or heat reflecting coloration) offered by some flower types. Flying and thermoregulation require about 0.3 cal/min at 20° C, with more energy required at lower temperatures (Heinrich 1979a).

Plant species frequented by bumblebees may be classed as one of two general types: those with open, easily manipulated flowers and those with complex, zygomorphic flowers. Open flowers usually have small rewards (i.e. 0.015 cal/flower in Vaccinium), although they may occur in large numbers on single inflorescences. Complex flowers usually have larger rewards and occur in fewer numbers. For example, Aconitum flowers may produce a cumulative nectar load of up to 24.0 cal/flower through the blooming period (Heinrich 1976a); the trumpet creeper, Campsis radicans, which produces approximately 110 cal/flower, is extremely rewarding for a temperate plant species (Bertin 1982). Nectar production may fluctuate through the flowering season, following diurnal patterns or varying with flower age and receptivity. In addition, pollinator visitation also influences apparent nectar load. A sample of 48 species of bumblebee flowers had an average standing crop of nectar of 0.24 cal/flower in individuals open to pollinators and an average of 2.88 cal/flower in flowers screened from pollinators for 24 hours (Heinrich 1976b). Although with experience bumblebees are capable of detecting minute visual or olfactory cues that distinguish rewarding from nonrewarding flowers of some species (Marden 1984), they do not have the ability to distinguish the reward level of a given species without first sampling it (Heinrich 1976a).

Cypripedium acaule produces no free nectar or any other apparent reward for its pollinators. As a probable result, visitation is low (Plowright et

al. 1980) and many flowers are never visited by pollinators, suggesting that reproductive success in this species may be pollinator limited. The breeding system of this species has not been documented, although a wide range of systems, ranging from apomixis and autogamy to self-incompatability have been demonstrated in other orchid species (e.g., Pogonia ophioglossoides: Thien and Marcks 1972, Encyclia cordigera: Janzen et al. 1980). To determine the breeding system and the extent to which pollen and resources limit long term reproductive success in C. acaule, estimates of temporal variation in fruit set (fraction of flowers setting fruit) over a five year period were determined for the Clinch Mountain population. Regional variation in fruit set also was estimated from data collected over two years at several sites in the southeastern United States, and pollination and defoliation experiments were conducted over a two year period. The importance of nectar as a pollinator attractant was tested by studying the effect of the artificial addition of nectar to flowers on insect visitation and fruit set in three populations.

Materials and methods

In the Clinch Mountain population (CIM), estimates of flowering and fruiting in 1981 were obtained by counting the persistent flower stalks and seed pods on the plants present in 1982. Although this sampling method excludes dormant plants and any adults which died between 1981 and 1982, such events are rare in this population (Chapter 3) and this probably would not greatly bias the sample. Since late frost damaged some flower buds each year, two measures of the population's reproductive status are pertinent: the fraction of the population having reproductive success (#fruits/#flower buds

produced) and the fraction of flowers successfully pollinated (#fruits/#flowers open to pollinators).

In addition to CIM, a total of nine C. acaule populations in the Southeast were sampled for fruiting success in 1984 and 1985 (Figure 8):

1. Stinking Creek, Tn (SC); USGS Jellico, TN-West Quadrangle, 550m elevation. Private property. Mixed chestnut oak and pine forest, heavily disturbed by southern pine bark beetle damage and lightly pastured.
2. Cross Mountain, Tn (CrM); USGS Block, TN Quadrangle, 885m elevation. Koppers Wildlife Management Area. Area 1: Chestnut oak forest, recently logged and bounded by surface mining area. Heavy shrub layer consisting of Vaccinium, Rhododendron and Kalmia. Area 2: Mixed oak forest bordered by surface mining area and Rhododendron thicket.
3. Chilhowee Mountain, Tn (ChM); USGS Kinzel Springs, TN Quadrangle, 365m elevation. Chilhowee Mountain Wildlife Management Area. Mixed white pine, hemlock and deciduous hardwoods. Light disturbance by Southern pine bark beetle, damage to pines, some windfall damage, light logging.
4. Greenbriar School, Tn (GB); USGS Wears Cove, TN Quadrangle, 610m elevation. Great Smoky Mountains National Park. Mixed pine, hemlock, and hardwoods. Light to moderate windfall disturbance.
5. Lake Chatuge, NC (LC); USGS Hayesville, NC Quadrangle, 610m elevation. TVA reservation. Pine forest. Bordered by fill dirt excavation.
6. Brasstown Bald, Ga (BB), USGS Brasstown Bald Quadrangle, 975m elevation. Chattahoochee National Forest. Mixed hardwoods and pine forest, heavy shrub layer of Rhododendron. Trail and road borders.

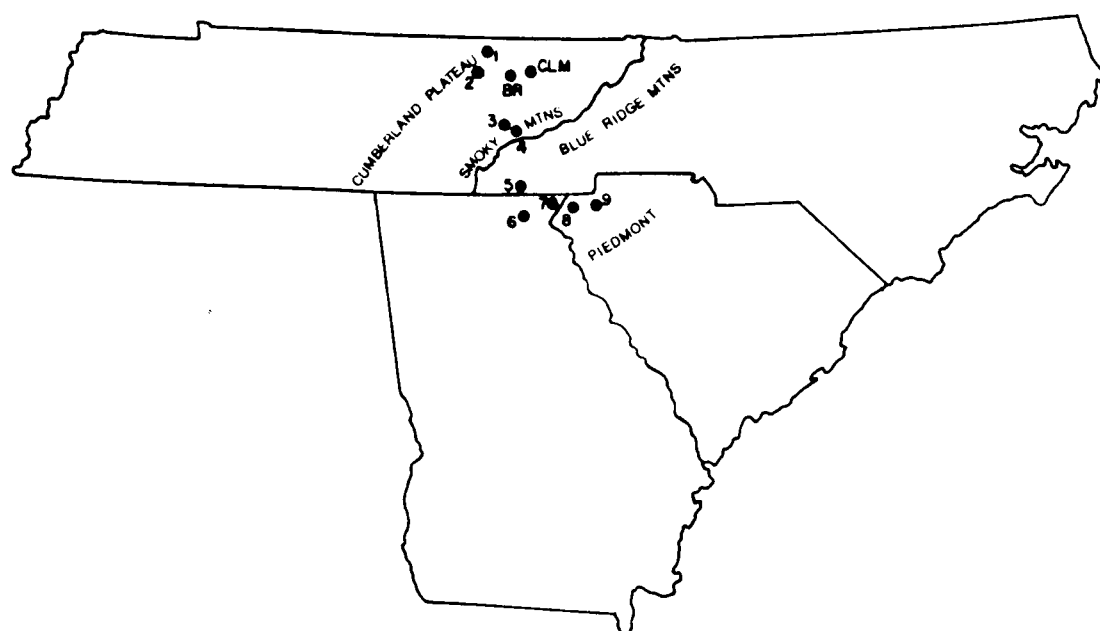


Figure 8: Locations of study populations in the Southeastern U.S.

7. Rabun Bald, Ga (RB), USGS Rabun Bald, NC-GA Quadrangle, 1160m elevation. Chattahoochee National Forest. Pine forest regrowth in clearing circa 1940.
8. Oconee Station, SC (OS); USGS Walhalla, SC Quadrangle, 335m elevation. Oconee State Park, Sumter National Forest. Mixed pine and hardwoods. Southern pine bark beetle damage and power line construction.
9. Lake Issaqueena, SC (LI); USGS Clemson, SC Quadrangle, 275m elevation. Clemson University Experimental Forest. Loblolly pine plantations.

Sites were chosen from areas of large known populations, using herbarium records from The University of Tennessee, Knoxville, The University of Georgia, Clemson University, and information from local contacts. Five sites were located northwest of the Great Smoky Mountains, the remaining five southeast. The populations were also stratified into three groups by elevation and three groups by latitude. After anthesis, the number of flowering and fruiting plants were recorded for each site. Four sites (SC, CrM, LC, and RB) were sampled only in 1985.

Pollination and defoliation experiments were performed on Clinch Mountain in area 3. In 1984, 300 flower buds were bagged to exclude subsequent pollinators. All plants were single shoot individuals. Each was marked with a numbered plastic stake. Pollination and defoliation treatments were assigned to 200 individuals in a 2 x 2 Latin square design. The remaining 100 individuals were maintained as controls.

As individuals were encountered, treatments were assigned systematically in the following order: outcrossed, outcrossed and defoliated,

control, selfed, selfed and defoliated, control. Initial leaf area did not vary significantly between treatments (ANOVA: $F_S=0.0455$, $p>0.05$, $df=2$). Each outcrossing experiment used pollen from one donor. Plants were defoliated by removing both leaves at soil level at the time of pollination. All treatments were performed during the week of May 9-15, 1984. Predation by rodents (Peromyscus sp.) and wind damage removed six individuals from the experiment, leaving 50 outcrossed, 49 outcrossed and defoliated, 48 selfed, 49 selfed and defoliated, and 98 controls.

In 1985, a census of all 300 plants was conducted, noting growth form (absent, one leaf, or two leaves), flowering state and leaf dimensions. Those individuals which bloomed in both 1984 and 1985 were pollinated again and an additional 100 flowering individuals not included in the previous year's experiment were hand pollinated. Treatments were assigned systematically as individuals were encountered. Half were outcrossed, half were selfed. The 65 original control plants which also flowered in 1985 were bagged to exclude pollinators, but not pollinated. Treatments were performed on April 28-May 1, 1985.

Nectar enrichments were performed at Clinch Mountain area 1, Cross Mountain area 1, and along Big Valley Trail in Big Ridge State Park, Tn (BR) (USGS White Hollow, TN Quadrangle; see Figure 8) during April and May 1985. A solution of 25% sucrose, which provides 1 cal/ml usable energy, was used as a nectar substitute. Doses of approximately 24 calories were used to provide a net energetic gain of 23 calories, based on an estimate of 3 minute handling time per flower for a Bombus queen (Heinrich 1979a). This reward is in the range of highly rewarding, complex bumblebee flowers. A 3cc B-D syringe was used to enrich each open flower by placing three 7.91 ± 0.77 ml

drops of the sucrose solution on the hairs at the back of the flower behind the stigma (Figure 9). The nectar doses were protected from the weather by the closed form of the flower and remained in position despite rain and heavy wind. Since insect visitation and pollination are rare events, no attempt was made to observe visitation events. Instead, each treated flower was tagged with a numbered pot label and scored for number of pollinia removed, the presence of visible pollen on the stigma and the development of fruit. At all three sites, the majority of receptive flowers in a given area were enriched. This included 110 flowers at CIM, 122 flowers at BR and 209 flowers at CrM. The Clinch Mountain sample was enriched five times during the period April 24-May 12, the Big Ridge sample four times during April 25-May 14, and the Cross Mountain sample twice, on April 27 and May 11. Control populations (CIM areas 2 and 3, CrM area 2 and ChM) also were sampled on a single day near the end of anthesis for pollinia removal, pollen deposition, and fruit set. The results were compared to those for the enriched group at that site sampled on the same day. The BR population, which was not large enough to provide an adequate control group, was paired with ChM which was similar in spatial distribution. Repeated sampling for pollinia removal in the enriched groups occurred until all flowers had withered and further pollinator visitation was impossible. Final determination of fruit set occurred after the ovaries of pollinated flowers had begun to swell and unsuccessful inflorescences had fallen from the flower stalk (CrM, May 25; CIM, May 27; and BR, June 4).

Results

Adaptive floral display. The production of multiple flowers by a single genet may increase the apparency of that genet and increase its reproductive

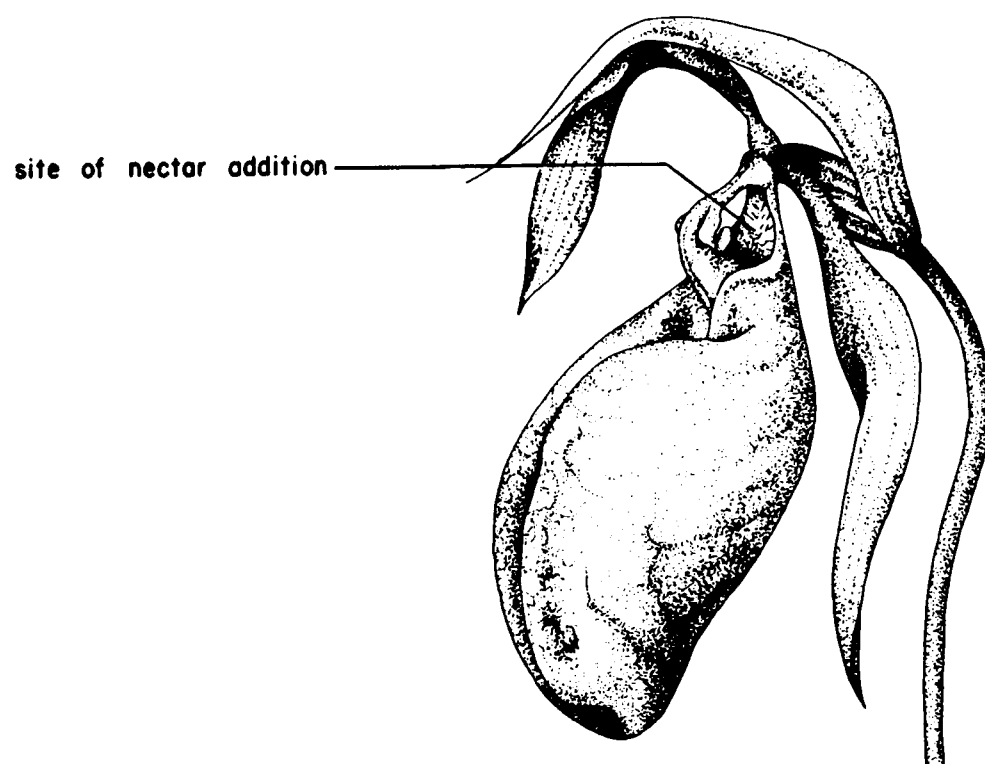


Figure 9: Nectar addition site.

success. If the increase in reproductive success is disproportionately large in relation to the increased investment in flowers, the production of additional flowers is referred to as an adaptive floral display (e.g., Schemske 1980). There is no evidence that the production of multiple flowers by C. acaule has more than a linear effect upon genet reproductive success (Table 22). In other words, all flowers produced by a population in a single year have essentially the same probability of setting fruit.

Temporal variation in fruit set. Temporal differences in flowering phenologies of woodland species, can affect bumblebee densities locally (e.g., Heinrich 1976c, Schemske et al. 1978) and hence, pollinator visitation and fruit set. Flower production remained fairly constant in C. acaule from year to year in the Clinch Mountain population. Fruit set ranged from 3.4% to 23.0% (Table 23) and was highly variable through time ($G=83.143$, $df=3$, $p<0.001$). Eliminating 1982, when fruiting success was very high, from the data set still yields significant variation in fruit set over years ($G=14.485$, $df=2$, $p<0.001$).

Table 22: Genet reproductive success and number of flowers produced.

year	flowers/genet	total #flowers	total # fruits	%	G	p
1982	single	299	63	21.1	1.434	>0.05
	multiple	141	37	26.2		
1983	single	226	22	9.7	0.714	>0.05
	multiple	214	16	7.5		
1984	single	230	9	3.9	0.220	>0.05
	multiple	150	4	2.7		
1985	single	277	15	5.4	1.165	>0.05
	multiple	203	16	7.9		

Table 23: Natural reproductive success rate (#fruits/#buds produced) and natural pollination fraction (#fruits/#receptive flowers) for *C. acaule* on Clinch Mountain

Year	#Buds	#Fruits set	%	#Flowers	#Fruits set	%
1981	334	34	10.2			
1982	489	101	20.7	440	101	23.0
1983	530	38	7.2	434	38	8.8
1984	382	13	3.4	379	13	3.4
1985	482	31	6.4	475	31	6.5
Total	2217	217	9.8	1728	183	10.6

There were 800 ramets which produced flowers in one or more years between 1982 and 1985. Of these, 250 (31%) flowered once, 196 (25%) flowered twice, 179 (22%) flowered three years out of four and 176 (22%) flowered every year. A total of 1883 flower buds were produced in this period for an average of 2.35 buds per ramet. Of these, 1738 survived to be available to pollinators, for an average of 2.17 receptive flowers per ramet. Average reproductive success was 0.23 fruits per reproductively mature ramet.

Spatial variation in fruit set. Despite the temporal variation in fruit set exhibited by the Clinch Mountain population, fruit set in six populations (CIM, ChM, GB, BB, OS, and LI) in 1984 (Table 24) was not significantly different between locations ($G=3.472$, $df=4$, $p=0.05$). Although the pooled probability of successful pollination at these six sites was higher in 1985 than in 1984, the only site recording significantly higher levels of fruiting was BB. There was no significant difference between fruiting success at these six sites in 1985 (Table 25).

Table 24: Natural fruit set for C. acaule in three southern states in 1984. No significant difference (G-test, $p > 0.05$).

Site	#Flowers	# Fruits set	%	Expected # ^a
GB	80	1	1.3	3.1
CIM	379	13	3.4	14.5
LI	139	6	4.4	5.3
OS	111	5	4.5	4.3
ChM	52	3	5.8	2.0 ^b
BB	47	3	6.4	1.8 ^b
Total	808	31	3.8	31.0

^a Expected number based on the intrinsic hypothesis of $p=0.038$.

^b pooled

Table 25: Natural fruit set for C. acaule in three southern states in 1985.

Site	#Flowers	#Fruit set	%	Change
GB	204	7	3.4	+2.1
CIM	475	31	6.5	+3.1
LI	1306	76	5.8	+1.4
OS	182	5	2.8	-1.7
ChM	77	5	6.5	+0.7
BB	70	19	27.1	+ 20.7 *
CrM	515	55	10.7	-
SC	140	20	14.3	-
LC	144	23	16.0	-
RB	153	19	12.4	-
Total	3266	260	8.6	

*significant increase from 1984 (G test, $p < 0.05$)

Fruit set following hand pollination. In 1984, only 13 of 379 (3%) flowers open to pollinators in CIM area 3 set fruit. Of 196 hand pollinated inflorescences, 182 (93%) set fruit. No controls set fruit. There was no difference in fruit set (Table 26) between selfed and outcrossed individuals (G test with Williams' correction (Sokal and Rohlf 1981): $G=0.002$, $df=1$, $p>0.05$). In addition, fruit set was unaffected by defoliation (Table 26; $G=0.298$).

The treatments performed in 1984 did influence reproductive output in the subsequent year (Figure 10). Fruit set in 1984 reduced an individual's probability of flowering from 65% in controls to 42% for plants pollinated but not defoliated ($G=10.69$, $df=1$, $p<0.005$). Defoliation further reduced flowering in 1985 to only one individual among the 90 defoliated plants setting fruit in 1984 ($G=27.404$). Growth form in 1985 was highly variable among defoliated plants (Figure 11) with more plants producing one leaf or remaining absent than nondefoliated plants. However, most individuals survived the resource depletion caused by fruit set and by defoliation.

In the second year of the study, hand pollinated individuals once again experienced a high incidence of fruit set. Ninety percent of the 100 new

Table 26: Reproductive success (#fruits/flowers pollinated) following hand pollination treatments on C. acaule in 1984.

	Pollinated	Pollinated & Defoliated	Total
Outcrossed	46/50	46/49	92/99
Selfed	46/48	44/49	90/97
Total	92/98	90/98	182/196

No significant differences between treatments (G-test, $p>0.05$).

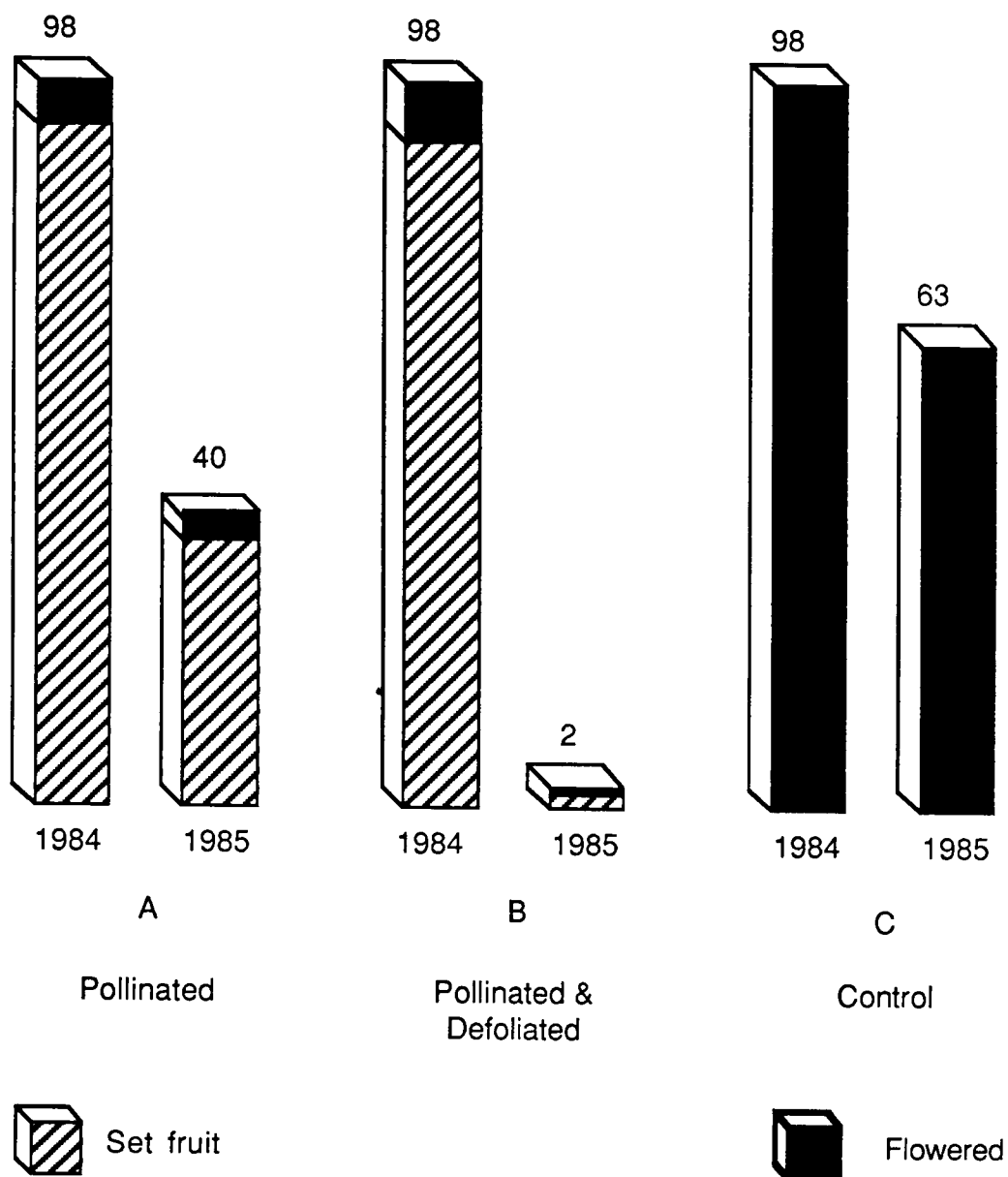


Figure 10: Reproductive output following hand pollination in 1984 and 1985.

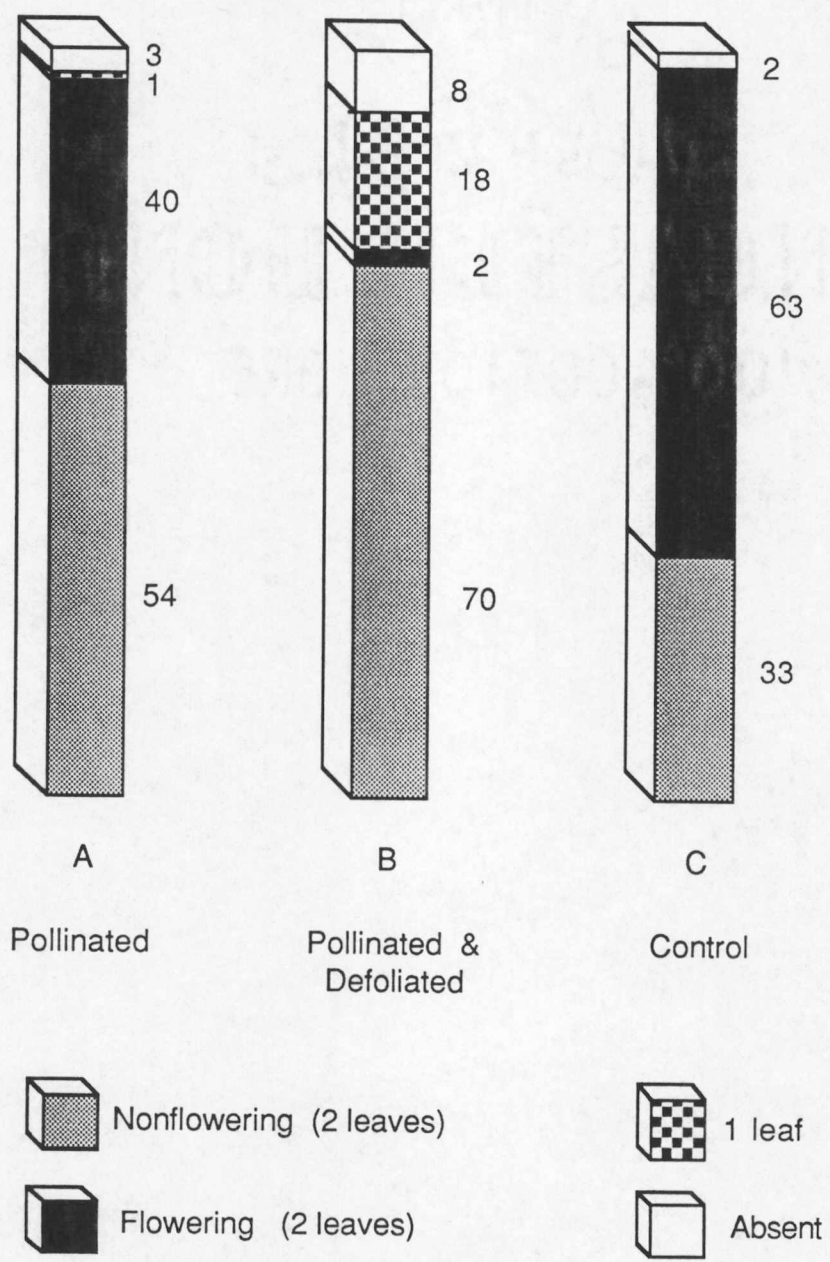


Figure 11: Vegetative form in 1985 following hand pollination in 1984.

individuals set fruit. Of the 40 individuals pollinated in both 1984 and 1985, 90% set fruit in 1985. This did not differ significantly from the 1984 sample ($G=0.564$, $p>0.05$, $df=1$). Despite a marked reduction in flower production, there was no subsequent reduction in fruit set.

Visitation and fruit set following nectar addition. Most terrestrial habitats are heterogeneous on a variety of spatial and temporal scales. C. acaule usually has a patchy distribution (Chapter 2). The distribution of most other forage flowers is neither uniform spatially or temporally (e.g., Heinrich 1976b,c; Schemske et al. 1978). There is evidence that the density of foraging bumblebees is proportional to the collective nectar levels of all species in a given area at a given time (Pleasants 1981). Bumblebees build hives and forage in their vicinity. Thus, it is not unreasonable to expect that insect visitation may vary on a local scale. In addition, numerous larger scale phenomenon, such as weather, land use or community structure, might also influence flower visitation on a regional scale. However, near the end of anthesis visitation was not significantly different either within control populations at CIM or CrM or between CrM, CIM and ChM (Table 27), averaging 24.9%. Nectar enrichment had a significant effect on visitation, pollinia removal and successful fruit set in both the Clinch Mountain and Cross Mountain populations (Table 27). Fruit set was influenced similarly by nectar addition and the subsequent increase in insect visitation (Table 28).

The reproductive success of an individual plant may be affected by the timing of anthesis in relation to other members of the same species (Thomson 1980). Numerous studies on the evolution of flowering times have noted that pollinators are usually in abundance and are competing for nectar in the early spring, while later in the season, nectar production outstrips the pollinators'

Table 27: Pollinator visitation in control and enriched populations May 11-17, 1985. CIM sampled on May 12, 1985; CrM sampled on May 11, 1985; ChM sampled on May 17, 1985; BR sampled on May 14, 1985.

Controls

Site	0 ^a	1	1p	1pf	2	2p	2pf	V ^b	total	%
CIM 2	293	48	0	31	7	0	0	86	379	22.7
CIM 3	140	38	1	9	3	1	0	52	192	27.1
CrM 2a	270	55	6	19	8	0	5	93	325	28.6
CrM 2b	60	12	1	3	2	0	0	18	78	23.1
ChM	64	6	0	5	2	0	0	13	77	16.9
Total	789	159	8	67	22	1	5	262	1051	24.9

Enriched

Site	0 ^a	1	1p	1pf	2	2p	2pf	V ^b	total	%
BR	96	17	0	7	2	0	0	26	122	21.3
CIM 1	68	19	0	17	1	0	5	42	110	38.2
CrM 1	56	37	4	23	29	4	22	119	175	68.0
Total	220	73	4	47	32	4	27	187	407	45.9

^a level of visitation. classifications are by # of pollinia removed (0, 1, or 2), presence of visible pollen on the stigma (p), and visible swelling of the ovary (f).

^b total # visited.

Table 28: Fruiting success in control and enriched populations, 1985.

	Site	# flowers	#fruits	%
Controls	ChM	143	12	8.4
	CIM	1127	78	6.9
	CrM	515	55	10.7
Enriched	BR	122	4	3.3
	CIM	107	21	19.6
	CrM	227	56	24.7

foraging abilities and plants compete for pollinators (e.g., Hocking 1968, Mosquin 1971, Heinrich 1975, Schemske et al. 1978, Zimmerman 1980). As nectar-producing species come into flower, pollinators may switch to more rewarding species (e.g., Heinrich 1976b, Pleasants 1981). In addition, pollinators quickly learn to avoid nonrewarding species. Thus, in nonrewarding species and to a lesser extent in rewarding species, visitation and a plant's probability of setting fruit usually should be greater in the early stages of flowering in the population and decrease through time (e.g., Dactylorhiza sambucina (Nilsson 1980), although, see Thien and Utech 1970). In the Cross Mountain enriched population, early flowers (open before May 11) received significantly more pollinator visits (122 of 175) than late flowers (28 of 56) and had significantly higher fruiting success (28.6% versus 11.1%).

Discussion

The large difference between fruit set under natural conditions and that following hand pollination ($G=520.608$, $X^2=7.879$, $p<0.005$, $df=1$) clearly shows that short term reproductive success in C. acaule is pollen limited. Lowered resource availability, through allocation of resources to fruits or through defoliation, affects reproductive success by lowering subsequent flowering. The lack of pollen delivery, however, has a much stronger effect. If potential fluctuations in juvenile establishment and mortality are ignored, then under normal rates of fruit set it would take an individual ten to twenty years to achieve the same level of reproductive success as that gained through just two years of complete pollination, a difference of an order of magnitude. Since fruit set reduces the probability that an individual will flower in

subsequent years but does not increase adult mortality, even individuals which fail to flower in the year following fruit set might be expected to resume flowering eventually. This ability to return to the reproductive class, coupled with low mortality and long life span would further increase the long term reproductive success of a population that was pollen limited.

Although studies of other pollen limited orchid species show similar high levels of fruit set following hand pollination (e.g. 100% in Goodyera oblongifolia: Ackerman 1975; 85% in Listera cordata: Ackerman and Mesler 1979; 85 to 97% in Encyclia cordigera: Janzen et al 1980; 69 to 93% in Tipularia discolor: Whigham and McWethy 1980; 99 to 100% in Platanthera blephariglottis: Cole and Firmage 1984), the question of subsequent resource limitation in these species has not been addressed. It is not surprising that resource availability acts upon the initiation of flowers in C. acaule and not upon fruit set. In species with low pollination rates selection should favor traits, such as self compatibility and efficient modes of pollen presentation, which could increase fruit set. Since it is pollen delivery that limits fruit set, traits that lead to pollinator visits that do not result in fruit set (e.g., excess flower production as a pollinator attractant, the production of functionally male flowers, self incompatibility or ovule abortion) should be disadvantageous. If other natural populations of C. acaule undergo pollinator limitation as extreme as that the study population routinely experienced, adaptations to control or alleviate resource limitations to reproductive effort have had little opportunity to evolve. In contrast, this species has several traits consistent with pollinator limitation: trap flowers, large pollen masses, self compatibility, and pollen presentation that prevents the collection of pollen for food, protects it from removal by grooming and guarantees its

delivery to a conspecific. Low fruit set is balanced by a long reproductive life span, high seed production and vegetative reproduction.

Since C. acaule produces no nectar, the addition of nectar to flowers may attract insects which are not normally pollinators of this species. Nevertheless, the increase in fruit set following nectar addition implies that no matter what the species of pollinator, the number of successful pollinations, and possibly the population's fitness, have increased. It follows from the "most effective pollinator principle" (Stebbins 1970) that under these conditions, selection should act to strengthen the morphological adaptations of the flower to the most common and effective pollinator. In particular, if nectar production attracts a new pollinator which increases fruit set, selection should not favor traits which exclude that new pollinator. Thus, any new pollinators attracted to a nectar-producing morph should become regular pollinators of the species as the morph spreads. If nectar production results in increased pollinator visitation and fruit set, why has nectar production not evolved in this species?

Summary

The pink lady's-slipper produces no nectar or other reward for its pollinators, chiefly large bodied bees of the genus Bombus. Visitation which results in the removal of pollinia (male function) is low, generally including about 20% of the flowers produced. Fruit set (female function) is also low, occurring in about 10% of the flowers produced. Reproduction is limited by pollen, resources and nectar, but pollen has the greatest long term influence on reproductive success.

CHAPTER 5

A GAME-THEORETIC ANALYSIS OF POLLINATION BY CHANCE

Game theory has become an important tool for evolutionary biologists seeking to understand a variety of questions ranging from animal behavior to the consequences of sex allocation (for a review, see Maynard Smith 1982). Since this technique focuses on assessing the relative success of individuals of different phenotypes (usually referred to as strategies), it provides a theoretical framework for studying the action of natural selection. While most research has focused on animal populations, some work has been done on growth form in plants (e.g., Riechert and Hammerstein 1983). Other life history traits important in plant species, such as energy allocation in hermaphrodites, timing of reproduction, dispersal, and seed dormancy, have also been analyzed with game theory (e.g., Hamilton and May 1977, Comins et al. 1980, Charnov 1982, Taylor 1985). Nevertheless, plant ecologists generally have not used this technique in studying the evolutionary consequences of life history traits. This may be due in part to the inherently anthropomorphic jargon associated with evolutionary game theory. Such jargon has recently come under criticism (Kramer 1984) for implying intent on the part of the organisms modeled and thereby misdirecting research. In addition to suggesting animal contests, this terminology also implies direct interaction between two individuals or at most between an individual and its nearest neighbors. However, it is equally appropriate to apply game theory to more diffuse, population-wide interactions where each individual plays against the entire population.

One such population-wide game which is evolutionarily important in many species of angiosperms is the attraction of pollinators. Sexual reproduction is usually important for the long term survival of plant populations, even in species which are capable of vegetative reproduction (e.g., Williams 1975). In addition to the potential genetic benefits of sexual reproduction, seed production also enables plant species to disperse to new habitats and to survive severe conditions. Insect visitation frequency may have a profound effect on reproductive success in pollen-limited species. Thus, variation in traits which influence visitation, such as nectar production, olfactory cues, visual cues, or flower production, might be expected to lead to differences in fitness. When pollinators cannot detect reward levels prior to visiting a flower, variable rewards may cause an animal visitor to abandon a species or to visit it more extensively. Energy devoted to rewards reduces the amount of energy available for vegetative and sexual reproduction. This may result in a reduction of the number or size of seeds or in reduced seed or seedling viability or vigor, or both. Thus, the cost of an increased reward must be counterbalanced by increased visitation and subsequently, increased fruit set. Many species produce variable amounts of nectar either at the population or individual level (e.g., Aconitum columbianum, Brink and deWet 1980) and there are examples of nectarless populations of normally rewarding species (e.g., Lobelia cardinalis, Brown and Kodric-Brown 1979).

Not all plant species produce nectar. Many nectarless species are wind or water pollinated and are thus independent of animal vectors for reproduction. Some species offer some other reward to their pollinators, such as pollen, oil, pheromones, or oviposition sites. Other nectarless species are mimics, which attract pollinators by mimicking rewarding species or even the

mates of their insect visitors (e.g., Faegri and van der Pijl 1966). However, there are some nonrewarding species which apparently are not mimics, the simple deceptive species (Boyden 1982). The associated pollination syndrome is called pollination by chance (Stoutamire 1971). Most pollinators exhibit foraging behaviors that limit their contact with non-rewarding flowers. Thus, it may seem counterintuitive that some plant species which never produce any reward may persist despite their dependence upon pollinators for fruit set. Both mimicry and pollination by chance are common in the Orchidaceae and Asclepiaceae, families which share the traits of pollen presentation in pollinia, large numbers of ovules and seeds, and specialized pollinators (Dafni 1984). It has been hypothesized that simple deception may arise from resource-limited nectar-bearing species (Heinrich 1983). However, it will be shown from a relatively simple game-theoretic model of insect foraging patterns that resource limitation is not necessary for the evolution or persistence of pollination by chance and only serves to speed the species towards fixation at the nectarless state by increasing the relative fitness of the nonrewarding phenotype.

Games Against the Field

Classical game theory was developed to analyze conflicts of interest between individuals. The name is due to the similarities to the so-called parlor games in both formulation and solution. It is of particular use in instances when the benefits accrued to an individual depend upon the behavior of other individuals in the population. Since natural selection acts upon individuals and individuals can only control their own actions, it is assumed that cooperation does not occur. Games are formalized as contests

between individual players. Each player has the option of adopting one of a range of behaviors, or "strategies." The choice of strategy is determined by the relative benefit, or "payoff," of each strategy; the "goal" of each player is to maximize their payoff under any array of strategies played by their opponents. In evolutionary games, this goal corresponds to the action of natural selection on phenotypes and the payoff is usually expressed in terms of Darwinian fitness. The solutions to these games are the strategies which lead to maximum payoffs. If a strategy, I , exists such that the adoption of any other strategy leads to lower relative fitness, I is called an evolutionarily stable strategy, or ESS (e.g., Hamilton 1967, Maynard Smith 1982).

Although much of classical game theory has focused upon two player games, the results may be extended to cover the interactions of entire populations. In this case, an individual's payoff depends upon the strategies played by every other member of the population. The analysis of playing the field is not as straightforward as that of two-player games; however, the existence of an ESS is guaranteed under the following conditions (Maynard Smith 1982, Riechert and Hammerstein 1983):

strategy I is an ESS if either

- i. $W(J,I) < W(I,I)$ for all $J \neq I$ or
- ii. if $W(J,I) = W(I,I)$, then for small q , $W(J,P_{q,J,I}) < W(I,P_{q,J,I})$,

where $W(J,I)$ is the fitness of a single J strategist playing against a population of I strategists and $W(J,P_{q,J,I})$ is the fitness of a single J strategist in a population with a small fraction q of J strategists, where q is greater than $1/(\text{population size})$. Condition i implies that an individual of type I cannot

increase its fitness by changing to strategy J, while condition ii states that even if the fitness of a single mutant J is indistinguishable from that of the majority strategy I, the fitness of the mutant is lower than the majority once the frequency of the mutant reaches some critical low proportion, q .

The Pollination Game

Pollination will be viewed here as a modified game against the field, where within a single species, every individual flower competes with every other flower for pollinators. The fitness of each flower (and ultimately the plant of which it is a part) depends upon the collection of phenotypes in the entire population. In choosing which flowers to visit and when to leave the population, the pollinator serves as a powerful "selection machine," determining the reproductive success of individuals of each type. In this version of playing the field, the population size is assumed to be finite (m). Since interactions between strategies are population-wide, mutant individuals can alter greatly the fitness of all individuals in the population. Thus, in order to determine the existence of an ESS, one may no longer compare the fitness of a single mutant, J, in a population otherwise composed of strategy I to the average fitness of strategy I in a pure population, since the absolute fitness of the mutant may be less than that of an I strategist in a pure population but greater than that of an I strategist in the perturbed population. In this circumstance, the mutant phenotype would become more highly represented in the population in future generations and, by definition, strategy I could not be an ESS. Instead, the average fitnesses of both mutant J and the majority strategy I must be compared under the perturbed conditions. For example, in order for nectar-bearing individuals to invade a population of

otherwise nonrewarding individuals, the following inequality must hold:

$$F_N(1, m-1) > F_D(1, m-1) \quad (1)$$

where $F_N(1, m-1)$ is the average fitness (i.e., number of seeds produced) of a single nectar-producing individual in a population of one nectar producer and $m-1$ nonrewarding plants, and $F_D(1, m-1)$ is the average fitness of a nonrewarding individual in the same population. A phenotype J is an ESS if the fitness of individuals having trait J is always greater than those having other phenotypes, no matter what the mixture of phenotypes is in the population. It should be noted that in the case of finite, integer population sizes, the fitnesses of each phenotype can be calculated for each possible mixture of phenotypes and it is not necessary to formulate analytical expressions for F_N and F_D in order to compare them.

Model Assumption

In order for traits influencing pollinator visitation to affect fitness, the species under consideration must be subject to pollen limitation. In general, the fitness of a particular pollinator attraction strategy is given by the expected number of fruit set by individuals of that strategy times the number of seeds per fruit divided by the number of individuals of that type. If the attraction strategy also influences seed or seedling survival (i.e., through reduced seed size or dispersal ability), it may be necessary to include a survivorship factor. Since orchids produce seeds of very small size containing no endosperm, for the purposes of this discussion, seed size and survivorship are assumed to be fixed for the species. The dispersal ability of these wind-borne seeds is

also assumed to be fixed, so differences in seedling survivorship due to dispersal and other spatial interactions are ignored. In addition, the reproductive capacity of all individuals will be assumed to be equal and the total energy available for reproduction fixed. Within a single species or population there are two potential phenotypes: 1). nonrewarding and 2.) rewarding. The two phenotypes are otherwise indistinguishable. In general, nectar production increases the probability of pollinator visitation and subsequent fruit set. However, nectar production uses some fraction, n , of the total energy allocated to sexual reproduction, resulting in a reduction of the number of seeds per fruit. The "pollination game" is a contest between individual plants, not between plants and pollinators. Since a single nonrewarding species in a community of rewarding species will have little impact on pollinator fitness (Feinsinger 1983), pollinator foraging rules will be assumed to be constant. In addition, the pollinator must be capable of distinguishing between species and assessing the level of reward. Although pollinator constancy (the degree to which a pollinator specializes on a single species during a single foraging bout) is not necessarily assumed to be perfect, it must be taken into account in determining the number of successful pollinations. A suite of animal vectors may act as a single effective pollinator type as long as each possesses a similar foraging behavior and pollen delivering ability. Thus, an individual's probability of setting fruit will be determined by the pollinator's foraging behavior.

A Special Case

Since the payoffs in the pollination game are determined by characteristics of the plant and pollinator, consider the case of Cypripedium

acaule. The pink lady's-slipper is highly pollen limited and most flowers are never visited by pollinators. The deposition of pollen almost always results in fruit set, but usually only a bee already carrying pollen can pollinate a flower. Although the artificial addition of nectar increases both visitation and fruit set, this species produces no nectar (Chapter 4). The principal pollinator, the bumblebee, samples a variety of species before specializing on a few highly rewarding ones (Oster and Heinrich 1976, Heinrich 1979b). However, these bees will normally visit a nonrewarding species several times (generally less than 10) before abandoning it completely. This behavior is assumed to be favored for two reasons: the reward received from complex, zygomorphic flowers usually increases with foraging experience (e.g., Heinrich 1979b, Lavery 1980) and nectar loads vary with flower age and frequency of visitation by other pollinators, which may cause some nectar-producing plants to appear to be nectarless (e.g., Pleasants and Zimmerman 1979, Brink 1982). Both nonrewarding flowers and flowers from which the reward has been removed will be referred to as "blanks." In order to determine whether pollination by chance is an ESS for C. acaule, it is necessary to formalize the foraging behavior of its pollinators. Two simple rules for foraging are proposed: "abandon after first blank" and "abandon after k blanks," $k > 1$.

"Abandon After First Blank."

Since C. acaule is adapted morphologically to deposit and remove pollinia efficiently from its pollen vectors and since a flower has only two pollinia to be transferred, little, or no reproductive benefit would be accrued by a plant that is visited repeatedly by a pollinator. Nectar production is expensive from an energetic standpoint (for a review, see Vogel 1983). If a

nectar producing morph existed, natural selection would favor individuals which ceased this energetic expenditure as soon as pollination occurred. Under the simple rule "abandon after first blank," a bee should avoid a species after visiting a single flower from which it receives no reward (a "blank") and never visit individuals of that species again. This is a "success runs" experiment. Given a mixed population of nectar producing and nonrewarding individuals, a bee may avoid a species for several reasons. First, a pollinator may immediately visit a nonrewarding plant and avoid the species as soon as it exits the first flower (Figure 12). In this case, no pollination has occurred and thus no fruit are set or pollinia transferred. Secondly, the pollinator could first visit several different nectar producers before visiting a nonrewarding plant (Figure 13). In this case, all nectar producers visited, except the first one, will set fruit (female function) and all nectar bearers will donate pollen (male function). Since the nonrewarding individual is the last member of the species visited, it will set fruit but not donate pollen. The last pollen donor will father an increased number of offspring since the nonrewarding plant produces more seeds than a nectar producer. Because the pollinator removes nectar when it is encountered (if all nectar has been removed), the pollinator cannot distinguish between blanks of the nonrewarding phenotype and blanks which were once nectar producing. There are two series of events which could lead to this situation. If the first flower is revisited (Figure 14), each flower will set fruit and each will donate pollen. On the other hand, if some other flower is revisited (Figure 15), the first flower will not set fruit and the next to last flower visited will not donate pollen, since the revisited flower has already set fruit. This behavior can be summarized best in a game tree (Figure 16). The resulting fitnesses

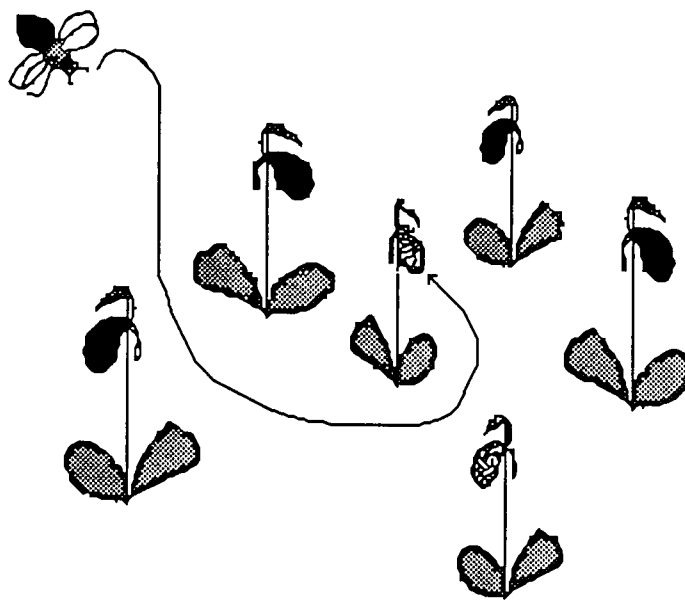


Figure 12: Foraging path 1, avoidance due to an immediate encounter with a nonrewarding flower. (Stippled flowers are nonrewarding, darkened flowers produce nectar).

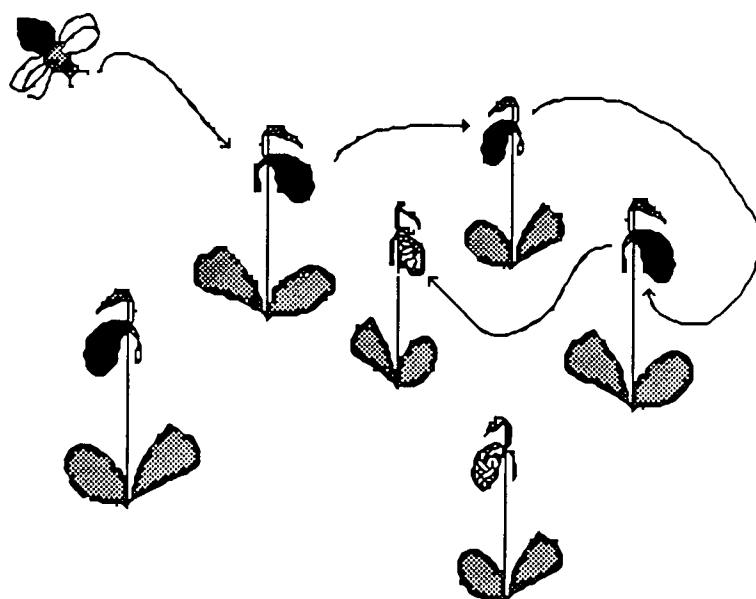


Figure 13. Foraging path 2, avoidance due to an eventual encounter with a nonrewarding flower.

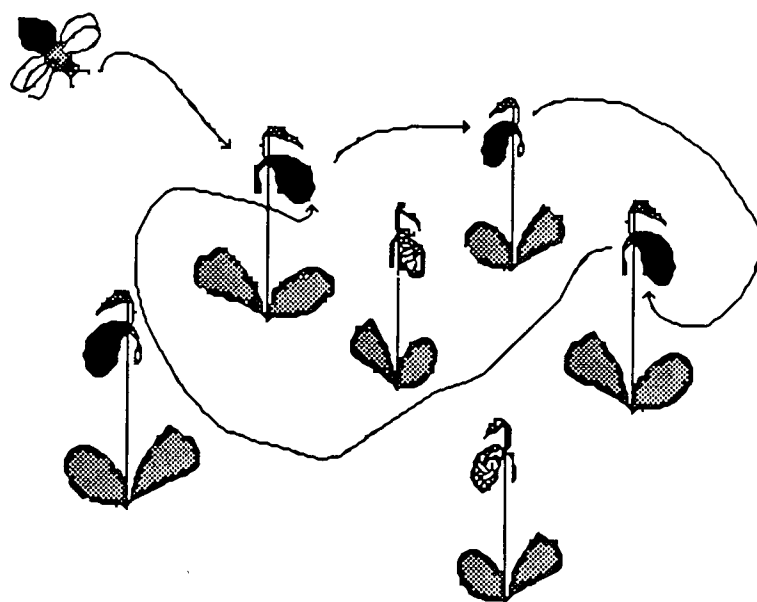


Figure 14: Foraging path 3, avoidance due to revisitation of first flower.

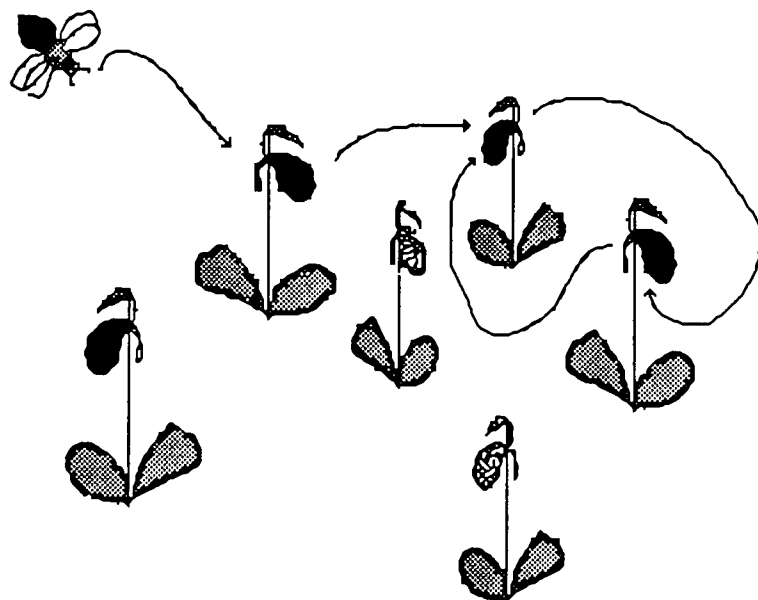


Figure 15: Foraging path 4, avoidance due to revisitation of second or subsequent flower.

revisit other revisit #! visit nonrewarding

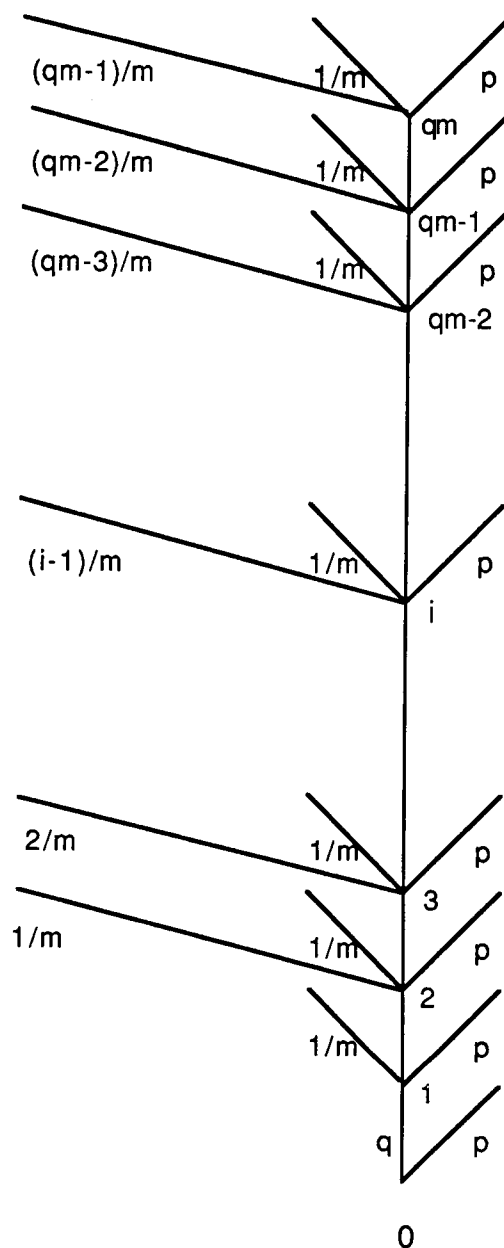


Figure 16: Game tree for the rule "Abandon after first blank"

can be described conceptually as

$$F_D = \Sigma \{P(\text{visiting } i \text{ rewarding flowers} \mid \text{last flower is nonrewarding})\} \\ \times \{P(\text{visiting a nonrewarding flower})\} \\ \times \{\text{\#fruits sets}/2\} / \{\text{total \#nonrewarding flowers}\}$$

and

$$F_N = [\Sigma \{P(\text{visiting } i \text{ rewarding flowers} \mid \text{last flower is nonrewarding})\} \\ \times \{P(\text{visiting a nonrewarding flower})\} \\ \times \{\text{relative seed production}\} \\ + \\ \Sigma \{P(\text{visiting } i \text{ rewarding flowers} \mid \text{last flower is \#1})\} \\ \times \{P(\text{revisiting \#1})\} \times \{\text{relative seed production}\} \\ + \\ \Sigma \{P(\text{visiting } i \text{ rewarding flowers} \mid \text{last flower is a revisit but not \#1})\} \\ \times \{P(\text{revisiting flower other than \#1})\} \\ \times \{\text{relative seed production}\}] / (\text{total \#rewarding flowers})$$

where $\{\text{relative seed production}\} =$

$$\{(\text{\# fruits set by nectar producers} + \\ + \text{\#pollinia transferred to nectar producers}) \\ \times (1 - \text{reduction of seeds due to nectar production}) \\ + (\text{\# pollinia transferred to nonrewarding flowers})\} / 2.$$

These correspond to the following equations:

$$F_D = \sum \{P(i)\} (p/2) / pm \quad (2)$$

$$= q/2m$$

and

$$F_N = [\sum \{P(i)\} p \{(1-n)(i-1) + 1/2\} \\ + \sum \{P(i)\} \{1/m\} i (1-n) \\ + \sum \{P(i)\} \{(i-1)/m\} \{i-1\}\{1-n\}] / qm, \quad (3)$$

where

$$P(i) = [(qm)/(qm-i)!] (1/m)^i$$

is the probability of visiting i rewarding individuals before abandoning the species, m is the population size, p is the fraction of the population which is nonrewarding, $q = 1 - p$ is the fraction of the population which is rewarding, and n is the fraction of seed output devoted to nectar production. Under this foraging rule, the average fitness of the nonrewarding individuals is always less than 0.5, due to the fact that male function is never realized. In order for pollination by chance to be favored over nectar production, the energetic cost of producing the nectar (n) must be large. Exact values depend upon the population size (m) and the proportion of nonrewarding plants (p), but in general, if $n > 0.5$, the nonrewarding phenotype will spread. In other words, if a nonrewarding plant is capable of producing at least twice as many seeds as a nectar-bearing plant, nonrewarding individuals will be able to invade the population. Although energy allocation studies of reproduction do not usually report the partitioning of energy into nectar, flowers and fruit, one study of nectar production in Asclepias quadrifolia (Pleasants and Chaplin 1983) estimated that approximately 30% of the energy devoted to flowering is

allocated to nectar production; the proportion of total reproductive energy devoted to nectar would be significantly less than 30%. The allocation of 50% of reproductive energy to nectar probably does not occur, even in highly rewarding flowers. Thus, under the rule "abandon after first blank," nectar production would be an ESS. Since the fitness of a population of all nonrewarding individuals would be zero under this rule, pollination by chance could never be an ESS.

"Abandon After k Blanks."

In general, even during the sampling period a bumblebee will not abandon a species the first time it receives no reward. Instead, she continues to forage, only discarding a species after a number of blanks have been visited. Nectar rewards inherently occur in patches (e.g., Pleasants and Zimmerman 1979). It may be possible, as a result, that bees which have received a high reward move shorter distances between inflorescences than bees which have received no reward (e.g., Thompson et al. 1982). Consider a collection of infinitely many patches of uniform type (i.e., fixed m and p). Assume that a bee which receives no reward will leave the patch but will not abandon the species until it visits k nonrewarding flowers. Assume also that the probability of returning to the same patch is 0.0. Once again, the fitness of each strategy is determined by the foraging behavior of the bee.

The dynamics in patch 1 are now slightly modified from the case of "abandon after first blank." If the bee follows foraging path 1 and visits a nonrewarding flower first, it will abandon the patch, but it will also carry pollen (male function) to the next patch visited. Following foraging path 2 and abandoning the patch by visiting a nonrewarding individual results in the

same fitnesses for nectar producers as under foraging rule 1, but once again, pollen is carried from the last individual visited to the next patch. If the bee abandons the patch by revisiting the first flower, all nectar producers visited have both male and female function, and the first plant also donates a second pollinia to the next patch visited. If some other flower is revisited, once again the first flower has no female function and the next to last flower has no male function, but the last flower sends a second pollinia to the next patch.

In subsequent patches, the first flower visited always has female function. Thus, nonrewarding individuals which are visited all have both male and female function. The fitness of nectar producers is only altered by the fact that foraging paths 3 and 4 are now indistinguishable. In the k^{th} patch, the last flower visited loses its male function, since no further flowers are visited. Equations (2) and (3) describe the "first flower" and "last flower" phenomena. In each of the remaining $k-1$ patches the average fitness of nonrewarding individuals is determined by the game tree shown in Figure 17 with corresponding equation

$$F'_D = \sum \{P(\text{visiting } i \text{ rewarding flowers} \mid \text{last flower is nonrewarding})\} \\ \times \{P(\text{visiting a nonrewarding flower})\} \\ \times \{\text{relative number of seeds}\}.$$

The fitness of nectar producers in these patches is

revisit other

visit nonrewarding

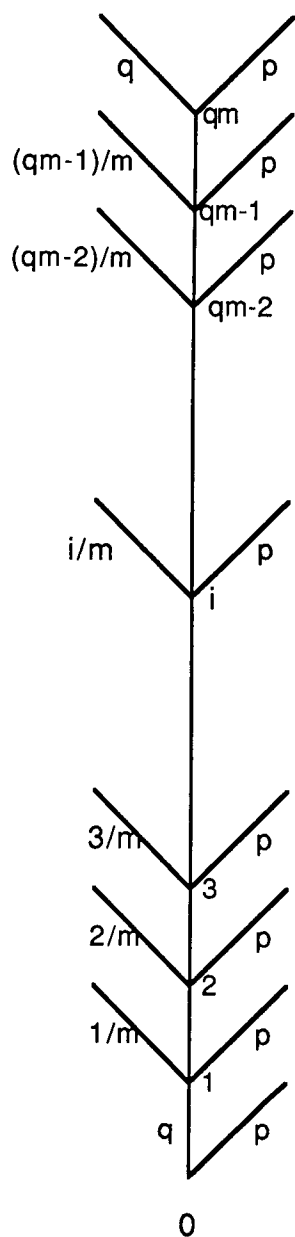


Figure 17: Game tree for second and higher deceptions under the rule "Abandon after k blanks"

$$\begin{aligned}
 F'_N = & [\sum \{P(\text{visiting } i \text{ rewarding flowers} \mid \text{last flower is nonrewarding})\} \times \\
 & \{P(\text{visiting a nonrewarding flower})\} \\
 & \times \{\text{relative number of seeds}\} \\
 & + \\
 & \sum \{P(\text{visiting } i \text{ rewarding flowers} \mid \text{last flower is revisited})\} \\
 & \{P(\text{revisiting flower})\} \times \{\text{relative number of seeds}\}],
 \end{aligned}$$

where relative number of seeds =

$$\begin{aligned}
 & [\{ \# \text{ fruits set by nectar producers} \\
 & + \# \text{ pollinia transferred to nectar producers} \} \\
 & \times (1 - \text{reduction of seeds due to nectar production}) \\
 & + \{ \# \text{ fruits set by nonrewarding flowers} \} \\
 & + \# \text{ pollinia transferred to nonrewarding flowers}] \\
 & / (\text{total } \# \text{ flowers of type I}).
 \end{aligned}$$

Thus, the portion of the fitness of each phenotype as determined by the forager's behavior in the remaining patches is described by the following equations:

$$\begin{aligned}
 F'_D &= (k-1) \sum \{P(i)\} p (1/2 + \{q(1-n) + p\}/2) / pm \\
 &= (k-1) \{1/2 + q(1-n)/2 + p/2\} / m
 \end{aligned} \tag{4}$$

and

$$\begin{aligned}
 F'_N &= (k-1) [\sum \{P(i)\} p \{(i - 1/2) (1-n) + 1/2\} \\
 &+ \sum \{P(i)\} q i / m (i-1/2)(1-n)] / qm
 \end{aligned} \tag{5}$$

where the variables are defined as in equations (2) and (3). The relative fitness of the nonrewarding phenotype is given by

$$W(d,m,k,n) = (F_D + F'_D) / (F_N + F'_N), \quad (6)$$

where $d = pm$ is the number of nonrewarding individuals, m is the patch size, k is the number of blanks allowed before abandonment, and n is the allocation of reproductive energy to nectar.

Four patterns emerge. It may be shown analytically that as the number of blanks allowed increases, the relative fitness of nonrewarding individuals increases, i.e.,

$$\begin{aligned} \partial W / \partial k = & \{ p^2 / (1-n)^2 + \sum P(i) [p(1+p)(i-1)/q(1-n) + p(i-1) + i/m \\ & + (i(1+p) - q(i-1/2) + q^2/2)/qm(1-n)] \} / 2 [pk/2(1-n) + (k-1)p/2 \\ & + \sum P(i) \{ kp(i-1)/q + (i + (i-1)^2)/qm + (k-1)(i-1/2)i/m \}]^2 > 0. \end{aligned} \quad (7)$$

for all positive values of k , since $i(1+p) - q(i-1/2) > i(1+p - q) > 0$. As the reproductive cost of producing nectar, n , increases, the relative fitness of pollination by chance increases, i.e.,

$$\begin{aligned} \partial W / \partial n = & [p^2(k-1)^2/(1-n)^2 + (q + (k-1)(1+p))/(1-n)^2 \times \\ & \sum P(i) \{ kp(i-1)/q + (i + (i-1)^2)/qm + (k-1)(i-1/2)i/m \}] / \\ & 2[pk/2(1-n) + (k-1)p/2 + \sum P(i) \{ kp(i-1)/q + (i + (i-1)^2)/qm \\ & + (k-1)(i-1/2)i/m \}]^2 > 0. \end{aligned} \quad (8)$$

In an examination of all integer population sizes of less than 200 with the number of blanks allowed ranging between 2 and 15, for a fixed patch size and number of blanks before abandonment, as the number of nectar producers decreases, the relative fitness of the pollination by chance decreases, i.e.,

$$\partial W / \partial d < 0. \quad (9)$$

Under the same condition, as patch size increases, the relative fitness of nonrewarding individuals decreases, i.e.,

$$\partial W / \partial m < 0. \quad (10)$$

In general, equation (1), the condition required for nectar producing individuals to invade the population, is equivalent to $W(m-1, m, k, n) < 1$. Thus, there are three possible outcomes. If $W(1, m, k, n) < 1$, nectar production will be an ESS. If $W(1, m, k, n) > 1 > W(m-1, m, k, n)$, there will be a mixed population. If $W(m-1, m, k, n) > 1$, pollination by chance will be an ESS. If $W(1, m, k, n) = 1$, it is highly probable in larger populations that the invading nonrewarding strategist will eventually be lost from the population due to sampling effects. A similar result is true for the rare nectar producer if $W(m-1, m, k, n) = 1$.

Numerical Results

Since the relative fitness, W , can be computed for all possible mixtures of strategies in a given population of fixed patch size, a comparison of the effect of nectar levels and the effect of number of blanks allowed can be

made. Consider a patch size of 25 individuals. Fitnesses for two levels of nectar and four different numbers of blanks are given in Table 29. In this example, nectar production is the ESS if only 2 blanks are allowed and the nectar production level causes a 1% reduction in seed number. Pollination by chance is the ESS for 4 blanks when nectar causes a 10% reduction in seed set and for 10 blanks at either level of nectar production. In the remainder of the cases, there is a mixed equilibrium.

Relaxing the Model Assumptions

Certain model assumptions were made to simplify calculations. They are not essential to the solution of the problem. Patch number need not be infinite. If the forager is capable of remembering its position so that patches are not revisited (e.g., Heinrich 1979c), the model results hold as stated. Otherwise, the probability of revisiting a patch and the distribution of pollinia and fruits must be taken into consideration when calculating the fitnesses. Patch size and type need not be uniform. Again, uniformity is only a simplifying assumption. It is only necessary that the patch sizes and types are known. The model is applicable to other systems of pollinator limited plants and specialist pollinators with suitable changes in the fitness functions (i.e., plant traits control number of pollen transfers and fruits and/or seeds set per flower visited, while pollinator traits control the probability of visiting each flower).

Implications of the Game

The pollination game implies that the success of pollination by chance is dependent upon several factors, most importantly, pollinator foraging

Table 29. Relative fitness, W , of nonrewarding strategists in patches of 25 individuals for nectar levels, n , of 0.01 and 0.1 and 2, 3, 4, and 10 blanks before abandonment. Values in parentheses are for $n = 0.1$

#non-rewarding	#nectar	2 blanks	3 blanks	4 blanks	10 blanks
1	24	0.92235 (1.01458)	1.03814 (1.14196)	1.09513 (1.20464)	1.19622 (1.31584)
2	23	0.90445 (0.99490)	1.01930 (1.12123)	1.07562 (1.18318)	1.17516 (1.29268)
3	22	0.88834 (0.97717)	1.00256 (1.10282)	1.05835 (1.16419)	1.15662 (1.27228)
4	21	0.87376 (0.96114)	0.98766 (1.08642)	1.04305 (1.14736)	1.14025 (1.25428)
5	20	0.86052 (0.94657)	0.97434 (1.07177)	1.02945 (1.13240)	1.12672 (1.23939)
6	19	0.84841 (0.93326)	0.96240 (1.05864)	1.01734 (1.11908)	1.11300 (1.22430)
7	18	0.83729 (0.92102)	0.95164 (1.04681)	1.00651 (1.10716)	1.10163 (1.21179)
8	17	0.82701 (0.90971)	0.94192 (1.03611)	0.99679 (1.09647)	1.09151 (1.20066)
9	16	0.81745 (0.89920)	0.93309 (1.02640)	0.98803 (1.08684)	1.08246 (1.19071)
10	15	0.80851 (0.88936)	0.92504 (1.01754)	0.98012 (1.07813)	1.07435 (1.18179)
11	14	0.80009 (0.88010)	0.91766 (1.00942)	0.97293 (1.07022)	1.06707 (1.17378)
12	13	0.79213 (0.87134)	0.91086 (1.00194)	0.96638 (1.06301)	1.06049 (1.16654)
13	12	0.78454 (0.86299)	0.90456 (0.99502)	0.96038 (1.05642)	1.05456 (1.16001)
14	11	0.77727 (0.85500)	0.89872 (0.98859)	0.95487 (1.05357)	1.04915 (1.15407)

Table 29, continued.

#non-rewarding	#nectar	2 blanks	3 blanks	4 blanks	10 blanks
15	10	0.77028 (0.84731)	0.89326 (0.98258)	0.94979 (1.04477)	1.04424 (1.14867)
16	9	0.76352 (0.83987)	0.88813 (0.97695)	0.94508 (1.03959)	1.03975 (1.14372)
17	8	0.75694 (0.83263)	0.88331 (0.97164)	0.94070 (1.03477)	1.03564 (1.13920)
18	7	0.75052 (0.82557)	0.87875 (0.96662)	0.93662 (1.03028)	1.03186 (1.13504)
19	6	0.74423 (0.81865)	0.87441 (0.96185)	0.93280 (1.02608)	1.02837 (1.13121)
20	5	0.73803 (0.81184)	0.87028 (0.95731)	0.92921 (1.02213)	1.02515 (1.12767)
21	4	0.73191 (0.80511)	0.86632 (0.95296)	0.92582 (1.01840)	1.02217 (1.12438)
22	3	0.72585 (0.79843)	0.86253 (0.94878)	0.92261 (1.01488)	1.01940 (1.12134)
23	2	0.71982 (0.79180)	0.85887 (0.94475)	0.91957 (1.01153)	1.01683 (1.11851)
24	1	0.71381 (0.78519)	0.85533 (0.94086)	0.91668 (1.00835)	1.01442 (1.11587)

behavior. Although game theory cannot determine whether C. acaule has evolved to produce no reward or if this species has ever been rewarding to its pollinators, the model does demonstrate that pollination by chance can be optimal in some sense, given a certain pollinator foraging behavior.

An examination of other foraging rules which might better approximate Bombus behavior is needed. In particular, the decision of when to abandon a species (optimal diet choice, Pyke 1984) as well as the decision of when to abandon a patch (optimal patch departure, Pyke 1984) is probably based on more information than either previous foraging rule uses. Since bumblebees sample several species then rank them according to level of reward and specialize on the species which appear to be most rewarding, the average reward should be considered when determining whether to abandon the species. In a similar fashion, once the pollinator chooses to visit the species, average reward should also be used in the patch departure decision.

Further Applications

The structure of the pollination game makes it applicable to a variety of population-wide contests between a finite number of individuals. In particular, the evolution of Batesian mimicry, in which a generalist predator's foraging behavior determines the relative fitnesses of models and mimics, can also be modeled in this fashion. If the mimic occurs in great enough numbers to reduce the model's fitness, there are three strategies, model, mimic and nonmimic, even if model and mimic are not interacting in the traditional form of competition (an increase in species 1 causes a decrease in species 2 and vice versa). The equilibrium densities of each phenotype' can then be predicted from the model, provided that the life cycles of model and

mimic are similar. Clutch defense against generalist predators is another example of the finite game against the field (defending parents competing with non-defending parents) except that the defense strategy may influence the future reproductive success of the defending parent. The non-defending phenotype would benefit from predators learning to avoid defending parents.

CHAPTER 6

SYNTHESIS

The life history of Cypripedium acaule seems to be an amalgam of several related extremes such as pollination by deception and low fruit set, small seed size and large number of seeds, high juvenile mortality and long life span, and a fairly steady population size with episodes of high turnover. These traits interact at several critical stages in the life cycle of the pink lady's-slipper to determine whether an individual will eventually reproduce. At each stage, from germination to pollination and fruit set, a successively smaller subset of the population is selected, which may affect both the genetic structure of the population and patterns of energy allocation in individuals.

In terms of individual fitness, survival to reach flowering size is critical since only a small fraction of the population flowers. The production of large numbers of wind dispersed seeds allows a plant to spread its propagules over a variety of microhabitats. The long development period necessary for individuals to reach flowering size may result in few individuals living long enough to reproduce. Recruitment into the reproductive class occurs rarely, so the removal of flowering plants from the population may reduce the effective population size and thus the potential for genetic variation. Since pollination success is essentially constant and low in most populations, this will reduce the expected number of fruits and seeds. It is not known if population size is limited directly by the number of seeds produced, but the relative fitness of phenotypes should be strongly related to seed number.

Insect visitation is a local phenomenon which determines which individuals successfully reproduce in C. acaule. The number of potential

mates is limited by the foraging range and floral constancy of the pollinators. The foraging behavior of Bombus, which typically fly further between inflorescences sampled after receiving no reward, probably prevents the production of multiple flowers from giving a disproportionate advantage in C. acaule. However, as plants age, the probability of insect mediated self-pollination may increase as the genet produces additional flowering ramets, despite morphological adaptations which favor pollen exchange between flowers. Since the pink lady's-slipper is self-compatible, on the average, the production of additional flowers does increase the reproductive success of genets.

It has been suggested that simple deception in orchids such as Cypripedium acaule, Calypso bulbosa (Boyden 1982, Mosquin 1970), Arethusa bulbosa (Thien and Marcks 1972) and Calopogon tuberosus (Thien and Marcks 1972) represents a tradeoff between frequency of fruit set and the high reproductive potential (i.e., number of seeds produced) of successfully pollinated individuals. These species share several floral characteristics, such as large, usually solitary, pink flowers and yellow or white sterile staminodes which serve as both false nectar guides and support for the pollinators. These nonrewarding species are all visited by Bombus and have low levels of visitation and fruit set. Pollinator limitation in these species may maintain populations at lower sizes than might otherwise be expected. Small population sizes would serve to reduce selective pressure on the pollinators to develop species-specific avoidance mechanisms (Stoutamire 1971). The game theoretic model of pollination by chance does predict that the relative fitness of nonrewarding individuals will decrease with an increase in the number of flowers in the pollinator's foraging range. However, the number of

contacts between these nonrewarding plants and individual pollinators will be small relative to the total number of encounters with rewarding species. It is doubtful that these rare encounters will result in selective pressure on the pollinators as long as they are capable of assessing the lack of reward and subsequently avoiding the nonrewarding species. In addition, it is the number of flowers in the foraging range (flower density), not the number of individuals in the population, that is under selective pressure. Thus, it is possible that pollination by chance may lead to the production of single large flowers capable of producing many seeds instead of inflorescences consisting of several smaller flowers, each capable of producing only a fraction as many seeds.

Successful pollination ultimately determines the representation of phenotypes to be acted upon by natural selection. As a direct consequence of low fruit set, a single fruit may represent a large fraction of the total reproductive output of a population in a particular year. Thus the effects of environmental variability (especially climate) on flower production and receptivity, pollinator activity, seed dispersal, germination, and seedling establishment and mortality on recruitment to the population may be significant, despite the relatively steady population size.

If long term reproductive success is not predominantly limited by resources, to what is the excess energy not utilized for reproduction allocated? The pollination and defoliation experiments discussed in Chapter 4 demonstrated that fruit set is unaffected by resource limitation. However, fruit set and defoliation did cause an increase in dormancy, and a subsequent reduction in leaf area and flower production the next season. Although the number of multishooted genets in the study population is small, it appears

from ramet recruitment and mortality data (Chapter 3) that additional ramets are produced in order to provide support for additional flowers. New ramets are usually maintained even in seasons when there is insufficient energy for all ramets to flower. The following hierarchy of energy allocation appears to hold:

1. Fruit production given successful pollination.
2. Perennation, even at the expense of not producing above ground parts for a season.
3. Vegetative shoots.
4. Flower production.
5. Additional ramets.
6. Additional flowers.

The production of fruit probably is favored over perennation due to the uncertainty of obtaining successful pollinations in the future.

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VITA

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She is a member of the Ecological Society of America, the American Association for the Advancement of Science, Phi Kappa Phi, Pi Mu Epsilon, and Sigma Pi Sigma. Ms. Cochran was employed by The University of Georgia Institute of Ecology on February 1, 1986.