1981

The effect of clone size on seed production in Canada goldenrod, Solidago canadensis L.

Luise Anne. Hermanutz
University of Windsor

NOTICE

The quality of this microfiche is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us a poor photocopy.

Previously copyrighted materials (journal articles, published tests, etc.) are not filmed.

Reproduction in full or in part of this film is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30. Please read the authorization forms which accompany this thesis.

THIS DISSERTATION
HAS BEEN MICROFILMED
EXACTLY AS RECEIVED

AVIS

La qualité de cette microfiche dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de mauvaise qualité.

Les documents qui font déjà l'objet d'un droit d'auteur (articles de revue, examens publiés, etc.) ne sont pas microfilmés.

La reproduction, même partielle, de ce microfilm est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30. Veuillez prendre connaissance des formules d'autorisation qui accompagnent cette thèse.

LA THÈSE A ÉTÉ
MICROFILMÉE TELLE QUE
NOUS L'AVONS REÇUE

THE EFFECT OF CLONE SIZE ON SEED PRODUCTION IN CANADA GOLDENROD, SOLIDAGO CANADENSIS L.

by

© Luise Anne Hermanutz

A Thesis
submitted to the Faculty of Graduate Studies through
the Department of Biology in Partial Fulfillment
of the requirements for the Degree of
Master of Science at The
University of Windsor.

Windsor, Ontario, Canada.

May 1981.

ABSTRACT

THE EFFECT OF CLONE SIZE ON SEED PRODUCTION IN CANADA GOLDENROD, SOLIDAGO CANADENSIS L.

by

Luise Anne Hermanutz

Flowering plants that form closely packed clones of genetically identical ramets present several potential problems involving seed production. Self-incompatible species may incur seed-set reduction due to increased intra-clonal pollinator foraging as a clone enlarges. This only redistributes geitonogamous pollen without achieving fertilization. Clones also represent large, concentrated masses of potential resource that, according to Root's (1973,1975) "resource concentration hypothesis", may sustain greater herbivore damage than non-aggregated plants (e.g. small clones).

Solidago canadensis L., the Canada goldenrod is a rhizomatous perennial that forms extensive clones, is self-incompatible and requires insect pollination. Its seeds are attacked by larvae of Coleophora spp. (Lepidoptera: Coleophoridae).

Fertilization and subsequent pre-dispersal seed predation rates in S. canadensis were monitored over a wide range of clone sizes during 1979. The number of insect

floral visitors per ramet per clone was recorded, representatives of each visitor class were collected, and their pollen loads assessed to determine probable pollinators. Visitor frequency increased with clone size. Many of these visitors were nectar and/or pollen robbers that did not achieve successful fertilization. The soldier beetle, Chauliognathus pennsylvanicus (DeGeer) (Coleoptera: Cantharidae) was found to be the major pollinator among the censused visitors. Another visitor, the blister beetle, Epicauta pennsylvanica (DeGeer) (Coleoptera: Meloidae) clipped and ate the stigmas. Epicauta consumed disc stigmas with greater frequency than ray stigmas. This activity pre-empted an average of 45 percent of the flowers per head from possible fertilization. Concomitantly, the early instars of Coleophora spp. consumed the ovules of flowers.

The percentage of flowers fertilized per head increased with increasing clone size. Variation in seed-set was as great between ramets within clones as between clones. This in part, resulted from variation in Epicauta stigma clipping and Coleophora ovule predation intensities within a clone. It may also reflect the distinctive foraging behaviour of Chauliognathus. Intra-clonal ramet density and distance to the nearest S. canadensis clone also contributed to overall variation in seed-set between clones.

The amount of predation closely followed the

fertilization pattern. The predation intensity was significantly, positively correlated with clone size. The older larval instars of Coleophora, which consume mature seeds, showed much stronger patch size differentiation than younger larvae. This may be due to the greater variability in seed-set per head in smaller clones, and hence higher larval mortality rates in these clones. Each larva utilized multiple heads.

These fertilization and seed predation patterns caused larger clones to have fewer seeds escaping per head than smaller clones. The greater ramet number and hence ovule production of these large clones more than balanced the increased predation intensity and therefore more seeds per clone were produced by the larger clones.

ACKNOWLEDGEMENTS

I would like to heartily thank my supervisor, Dr. Mike Weis for introducing me to the prairie, and for the free exchange of thoughts. Both Dr. R.T. M'Closkey and Dr. K.Y. Fung served on my committee and gave of their time freely. Thanks are extended to Dr. R.W. Cruden and S. Hermann (Dr.?) for their suggestions, and the stimulating exchange of ideas. I would like to thank Dr. R. Bovberg, Director of Iowa Lakeside Laboratory for allowing me to use the facilities during the summers of 1979 and 1980.

Mike Baillargeon, deserves special thanks for his valuable statistical advice, as does Dr. M. Starr. Margaret Lawrence kindly composed Figure 2.

Thanks to Denise Ferrari, Katherine Needham, Margaret Lawrence and Mike Weis for their friendship, which will certainly never be forgotten.

Merci to Robert Steele. Sometimes words can not convey the feelings of thanks properly.

I would like to acknowledge the financial support of Dr. M. Weis, and the Ontario Ministry of Colleges and Universities for stipends received through the Ontario Graduate Scholarship.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

The way in which a plant presents its flowers in both space and time determines many aspects of its pollination biology. The floral presentation determines 1) type and number of pollinators (Augspurger 1980, Heinrich 1975, Janzen 1971a), 2) their fidelity (Heinrich 1975) and hence 3) their relative pollination efficiencies. The relationship between presentation and pollinator foraging behaviour regulates gene flow and hence neighbourhood size (Schmidt 1980). The pattern of spatial and temporal presentation among populations and species establishes possible competition for pollinators within the plant community (Levin and Anderson 1970, Waser 1978a) and hence species flowering time (Heinrich and Raven 1972, Thomson 1980). Flowering pattern will ultimately determine how the fruits are displayed, which in turn may influence the intensity of pre-dispersal seed predation.

Species that present a synchronous flowering display are termed "mass-flowering" (Heinrich and Raven 1972). This flowering pattern was identified by Janzen (1971a) in reference to tropical trees and shrubs. One of the possible advantages of a massive bloom is thought to be attraction of large numbers of potential pollinators (Heinrich 1975). In temperate regions the "mass-flowering" phenology has been well characterized for only a few tree species (e.g. Catalpa, Stephenson 1980). However, clonal

species also present this phenological pattern. These plants reproduce vegetatively, and consequently form dense clones of genetically identical shoots. Because all members of the clone flower synchronously, the clone is analogous to a "mass-flowering" tree.

It would be energetically more profittable for a pollinator to visit multiple flowers and shoots within a single clone than to forage between clones (Heinrich 1975, Heinrich and Raven 1972). Travel time between flowering shoots would be minimzed and net caloric gain would be maximized (Pyke 1978a). Inter-clonal movement would therefore be expected to be infrequent, paralleling predictions of inter-plant movements in mass-flowering tropical species (Augspurger 1980, Frankie, Opler and Bawa 1976). This restricted pollinator movement could have two consequences depending on the breeding system: high seed-set but low amounts of cross pollination in self-compatible species, and low seed-set in self-incompatible species (Augspurger 1980, Heinrich 1975). Reduced seed-set in self-incompatible clonal species would result from intra-clonal foraging which only redistributes incompatible pollen between shoots. It is for these reasons that Carpenter (1976) and Heinrich (1975) have referred to the "mass-flowering" phenology as an "anomaly" or "conflict".

This spatial aggregation of resources is also likely to influence the population dynamics of the insects that

utilize the plant as a food source (Cromartie 1975). Once flowering has terminated and the seeds have matured, a clone presents a large, concentrated mass of potential resource to an herbivore (e.g. seed predator). Root (1973,1975) proposed, in his "resource concentration" hypothesis, that herbivores are more efficient in locating large, pure stands of their host plant. Specialized herbivores are more effectively "trapped" by these concentrated patches than are generalists that can utilize other available resources. Increasing densities of a host plant can lead to an increased herbivore load, and hence increased damage to the resident plant.

Another determinant of herbivore load is "associational resistance" (Tahvanainen and Root 1972). Associational resistance is the protection accruing to plants growing in a diverse community, as opposed to a natural or man-made monoculture. Natural communities usually present a wide array of plant species, in various mixtures. Interspersion of non-host plants with host plants decreases colonization efficiency and subsequent population density of herbivores. This reduction in host-finding ability can be mediated by the masking of a host's chemical stimuli, or by the physical distance between suitable hosts (Tahvanainen and Root 1972). Suspectibility to herbivore detection and the resulting damage, is determined by both size (or density) of the resource patches (e.g. clones) and their dispersion within

the community.

Solidago canadensis L. is a rhizomatous perennial that has the capacity to form extensive clones. Clone sizes range from those comprised of a single shoot to very old clones with hundreds of genetically identical shoots. S. canadensis is self-incompatible and requires insect-pollination (Werner, Bradbury and Gross 1980). Therefore it may also be referred to as a potential "anomaly", embodying conflicts similar to those encountered in tropical trees, both in its pollination and predation processes.

This study was undertaken to document the effect of clone size on seed-set and subsequent pre-disperal seed predation. Two basic questions were formulated: 1) Is there a detectable reduction in fertilization rate as clone size increases and the exploitable resources (pollen and nectar) become more spatially concentrated? 2) Since clones are analogous to monocultures of resource, does the specialist larval seed predator, Coleophora sp., respond to this "resource concentration", causing greater predation damage in large than small clones? Very few studies have examined herbivore response to host plant density and dispersion, outside the realm of agricultural (i.e. cultivated) systems (Ralph 1977, Raupp and Denno 1979). Both fertilization rates and pre-dispersal seed predation were monitored in S. canadensis clones, representing a broad range of sizes during 1979.

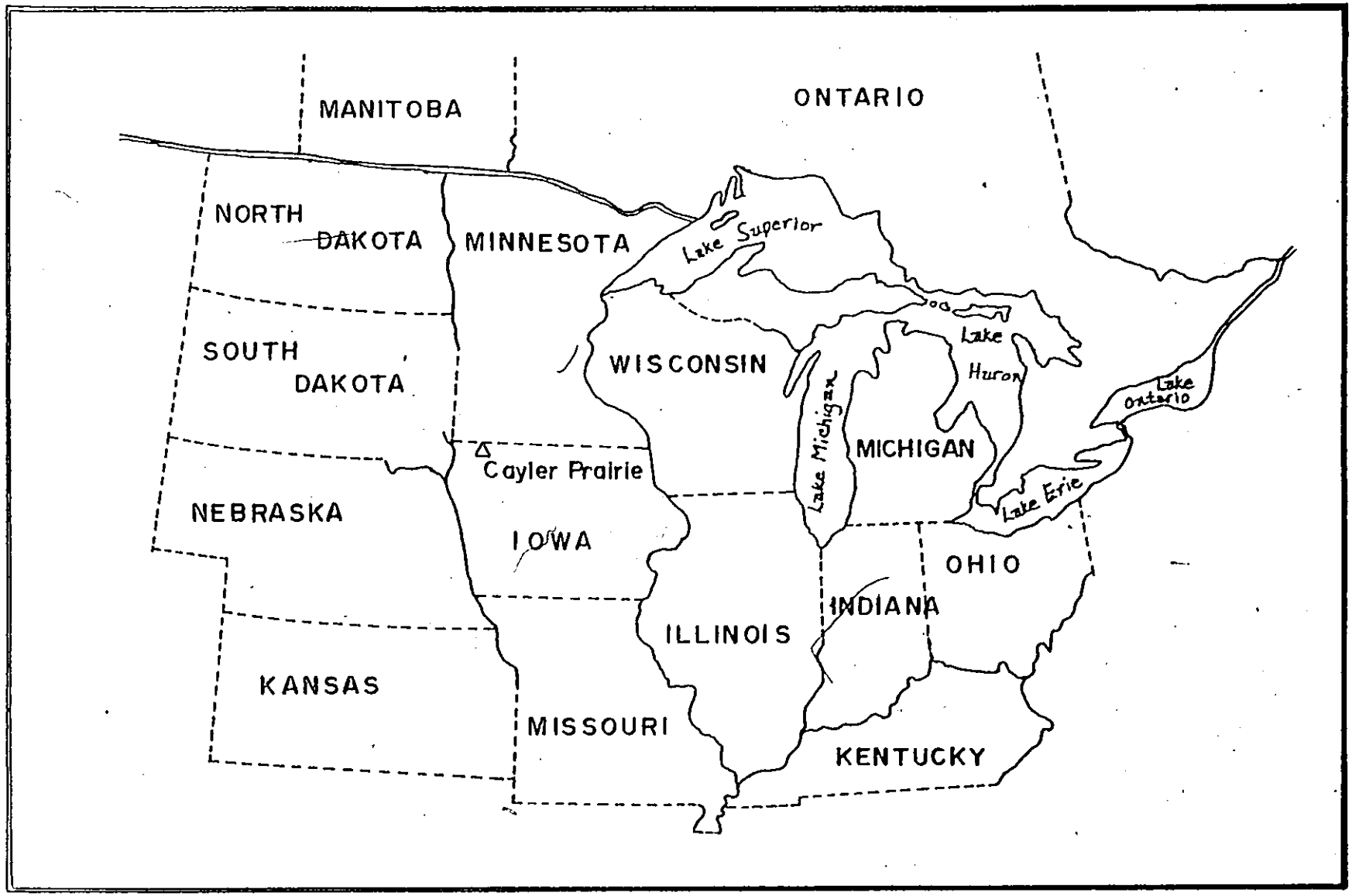
DESCRIPTION OF THE STUDY AREA

The field portion of this study was conducted in Cayler Prairie Preserve, a 64-hectare remnant of virgin tall-grass prairie, located in Section 17, Lakeville Township, Dickinson County, Iowa. (Fig.1). The Preserve consists of 42.1 ha that has never been plowed or grazed (Aikman and Thorne 1956), and a 22.7 ha section that was overgrazed before its incorporation into the preserve in 1960 (Platt 1975). Only the former area was used in this study.

The region is physically very diverse. It is part of the Altamont glacial moraine of the Wisconsin drift area (Hill and Platt 1975). The preserve is within the boundaries of an esker complex. Slopes range from 5-30° (Salisbury and Knox 1969 cited in Werner and Platt 1976). Soil types vary from sand and gravel loam in the upland areas to peat deposits in the deeper pot holes (Aikman and Thorne 1956). This heterogeneity has lead to the development of a complex stable plant community, with over 300 species of angiosperms (for a description see Aikman and Thorne 1956, Platt 1975, Hill and Platt 1975).

Figure 1

Map of the North Central States showing the location of Cayler Prairie Preserve in northwestern Iowa.


MANITOBA
ONTARIO
NORTH DAKOTA
MINNESOTA
Lake Superior
SOUTH DAKOTA
WISCONSIN
Lake Huron
Lake Michigan
MICHIGAN
Lake Ontario
Cayler Prairie
NEBRASKA
Lake Erie
IOWA
OHIO
INDIANA
ILLINOIS
KANSAS
MISSOURI
KENTUCKY

DESCRIPTION OF SOLIDAGO CANADENSIS L.

Solidago L. belongs to the tribe Astereae of the family Compositae. Of the more than 100 species included in this genus, all but a few are native to North America (Fernald 1950, Werner et al. 1980). Solidago and Aster are the most taxonomically complex genera in this very large family because of considerable intraspecific variation, geographic clines in characters, and frequent hybridizations among species (Fernald 1950).

S. canadensis L., the Canada goldenrod, is no exception to its genus designation and is highly variable. Species delineation depends on the authority consulted: two separate species or four to five varieties. (See Werner et al. 1980 for a discussion.) The Cayler Prairie population has been positively identified as S. canadensis (Werner and Platt 1976).

S. canadensis is a long-lived perennial that reproduces both sexually and asexually (vegetatively, via rhizomes). This rhizmatous habit forms a clone of interconnected, genetically identical aerial stems. The branching pattern of rhizome growth results in centrifugal spread and increasing absolute density within a clone with age (Smith and Palmer 1976). In Cayler Prairie clones can persist for hundreds of years (Werner et al. 1980). Clones with a diameter of up to 10 metres have been reported, although at this age the central portion is usually dead,

creating "fairy rings" (Werner et al. 1980). Harper (1977) uses 'genet' to represent the entire genetic individual formed by a single seed (i.e. the clone), and 'ramet' to describe each individual stem.

S. canadensis begins to flower in August and seed is set by October. Not all ramets within the clone flower. They must attain a minimum height of about 40 cm (Bradbury 1973, pers.obs.). In this study 21 to 78 percent of ramets within individual clones flowered. Bradbury (1973) reports flowering percentages of 34 and 54 in two clones found in old fields of different age.

The terminal inflorescence is a tightly packed pyramid-shaped panicle with recurved-secund branches (Gleason and Cronquist 1963). The individual subunits appear to be flowers but are themselves inflorescences. The head, or radiate capitulum, is an aggregation of both peripheral ray and central disc flowers typical of the Subfamily Tubuliflorae of the Compositae (Fig. 2a). Heads are very small (1.78 ± 0.035mm). In S. canadensis the rays are pistillate and fertile (Fig. 2b), and the discs are perfect and fertile (Fig. 2c). Each flower has an inferior ovary with one basal ovule and hence is one-seeded. The calyx is modified into a collar of hair-like plumes, the pappus (Fig. 2d).

The ray style branches are flattened and strap-shaped (length=0.73 ± 0.119mm n=41) and the stigmatic lines (areas receptive to pollen) are along the inside margin only. The

Figure 2

Floral structure of Solidago canadensis L.

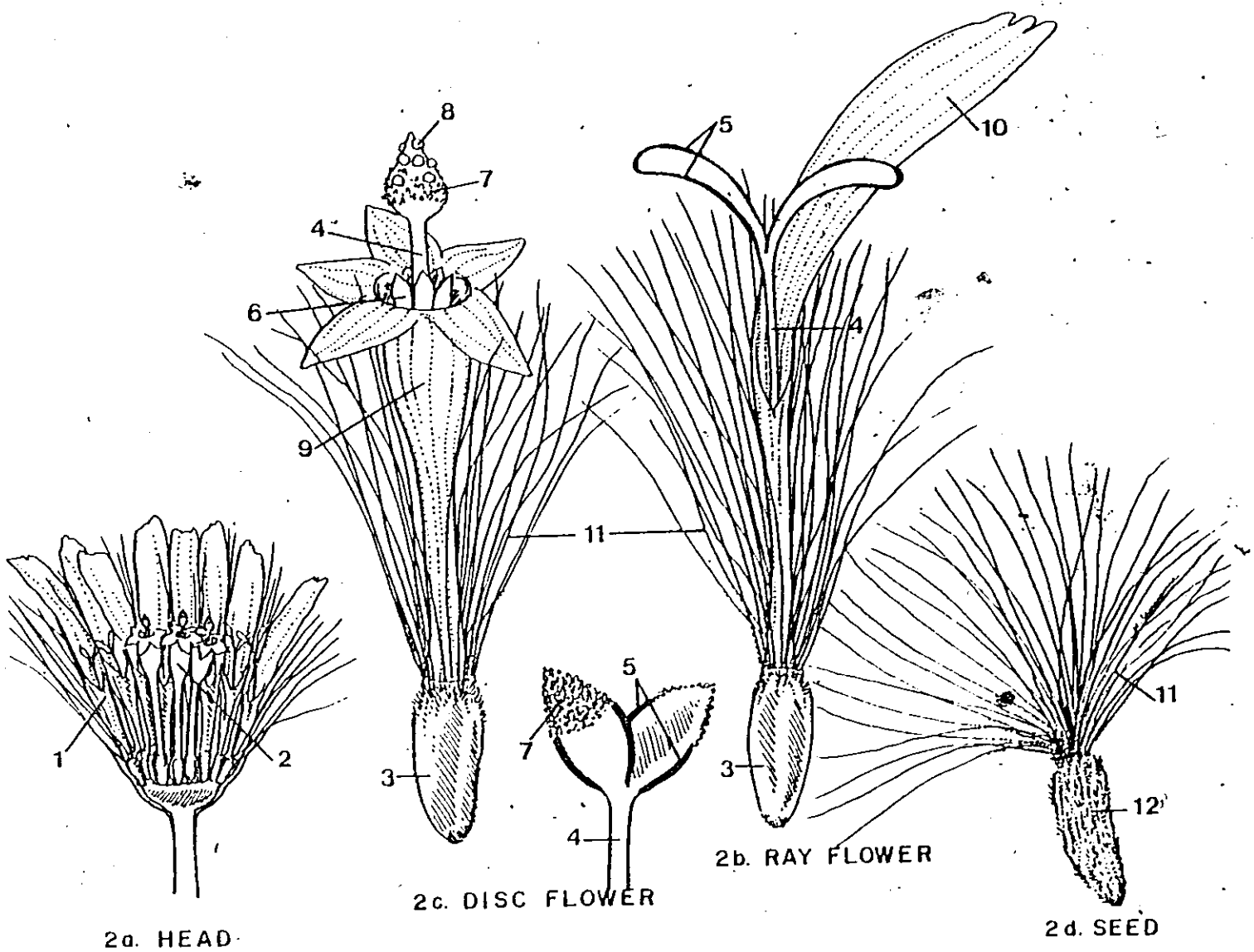
2a. Cross-section of a head.

2b. Ray flower.

2c. Disc flower.

2d. Seed.

1. Ray flower
2. Disc flower
3. Ovary
4. Style
5. Stigmatic lines
6. Anther ring
7. Sterile appendages
8. Pollen
9. Tubular corolla
10. Ligulate corolla
11. Pappus
12. Achene


1
2
2a. HEAD
8
7
4
6
9
3
11
2c. DISC FLOWER
5
7
4
5
10
4
3
2b. RAY FLOWER
11
12
2d. SEED

disc style branches are ovoid (length=0.787±0.0154mm n=34) and have sterile appendages (the "brush") on the outside upper half. Its stigmatic lines are along the inside margins of the basal portion (length=0.340±0.0118mm n=34). The base of the style in disc flowers is a nectary (Grau 1977).

The members of a clone all flower at the same time. Within a ramet the inflorescence matures from the base to the top. Each branch develops serially (inside to outside). The head has centripetal development, the ray flowers maturing before the disc flowers. Although the head as a whole is functionally protogynous ("female first"; because the ray flowers mature first), the individual disc flowers are protandrous ("male first"). The five anthers of a disc flower open inwardly and are fused to form a ring around the stigma. As the closed stigma elongates, it pushes through the ring, presenting the pollen above the flower like a "bottle brush". After this male phase is complete, the disc flower becomes female. This temporal separation of the sexes prevents autogamy (self-fertilization).

The duration of flowering in an individual head is seven to nine days, from the time the ray stigmas reflex to when the disc stigmas shrink back into the anther ring. The ray flowers all open within the first two days. The following day the disc flowers begin to open, one by one. The male phase lasts one to two days (pollen presentation);

then the style branches open and the flower is female for a few days (2-4). The ray stigmas stay reflexed for five to six days before shrivelling. The fact that stigma presentation occurs over a relatively long time period, exposes them to the possibility of multiple pollination visits.

This complicated sequence of flowering within heads, and the serial development of heads along branches of the ramet, means that there are 'zones' at the same stage of development (male and female), both in the heads and within the ramet.

S. canadensis is self-incompatible (Fryxell 1957 after East 1940, Mulligan and Findlay 1970, and Werner et al. 1980) and is therefore an obligate out-crosser. Since each ramet of a clone is genetically identical, pollen from another genet (clone) is required to accomplish fertilization. This means any ramet to ramet transfer of pollen is equivalent to geitonogamy, though strictly speaking geitonogamy is the transfer of pollen between flowers of the same plant (Faegri and van der Piji 1971). Both types of pollen transfer (within a ramet and between ramets) result in redundant pollinations that will not accomplish fertilization.

Like the majority of composites, S. canadensis is insect-pollinated and the head is the unit of attraction. Leppik (1970,1977) believes that the aggregation of solitary flowers into a head or 'pseudoflower' was a

response to the sensory mechanisms of these pollinators. Indeed, the head mimics a flower in design and function: the phyllaries protect and act as sepals; the ray flowers attract insects by acting as petals; and the disc flowers produce nectar (older,perpheral discs) and present pollen (younger,central discs) and represent the central portion of the flower (Faegri and van der Pijl 1971, Leppik 1977).

The dispersal unit in Solidago is actually an achene with attached pappus (Fig. 2d). The pappus acts as a parachute, enabling the seed to disperse great distances (Sheldon and Burrows 1973).

MATERIALS AND METHODS

1. Field Procedures

Clones of Canada goldenrod were chosen to represent a range in size (area in m^2), from single ramet genets (i.e. only one flowering basal stem) to the largest clones available. To ensure clonal integrity only clones with definable, non-overlapping peripheries were sampled.

The clonal area was determined by locating the centre of the clone and measuring the clonal radii every 30 degrees. The area of each 30 degree triangle was calculated, then summed to obtain total area (Appendix 1). For larger clones (diameter > 1m) this was a more accurate reflection of total clonal area, than the more traditional elliptical estimate because clones are polygonal (area= $\frac{\pi}{12}$ ab, where a and b are the radii). For smaller clones (radius < 50cm) the ellipse estimate was used. When the clone consisted of less than five flowering ramets the clone was considered round and the greatest distance between ramets was used as the diameter. The diameter of single ramet genets was assumed to be 6 cm, the size of the leaf shadow.

For each clone the total number of ramets and the total number of flowering ramets were counted. The vicinity of each clone was mapped with respect to location, distance to other S. canadensis clones, and distance to other simultaneously flowering species. These were other

fall blooming composites.

To assess possible differences in pollinator visitation frequency, as a function of clone size, and/or within individual clonal variation, large clones were divided into peripheral, middle, and central regions and small clones into peripheral, and central regions. No single ramet genets were used in this analysis. One ramet per region was randomly selected, tagged and its height measured. Weather permitting, each tagged ramet was monitored for flower visitors for a five minute period, twice a day (am/pm), from September 5 to September 10,1979. Most visitors were not identified taxonomically but placed into categories based on type (e.g.syrphid fly) and size (e.g. large)(Table 1). Number of visitors in each category was recorded, as well as food source exploited (nectar and/or pollen). Representatives of each visitor class were killed and mounted for subsequent body pollen counts. To discriminate between pollen types that might be found on the flower visitors, pollen samples from all clones and simultaneously flowering species were mounted in fuchsin glycerine jelly (Beattie 1971).

During the course of these observations I noticed that one of the beetle visitors, Epicauta pennsylvanicus DeGeer, foraged not only for nectar and pollen, but also clipped and ate the stigma of individual flowers. To assess the impact of this activity on overall seed output, randomly chosen ramets from each region were collected and preserved

Table 1. The importance of each visitor class.

VISITOR CLASS	MEAN # VISITS/5 MIN. /RAMET ±SE	% OF TOTAL VISITORS	N
Syrphid Fly (small)	2.66 ± 0.481	47.65	386
Syrphid Fly (medium)	0.12 ± 0.038	2.22	18
Syrphid Fly (large)	0.09 ± 0.032	1.61	13
Flies (small)	0.35 ± 0.067	6.17	50
Flies (medium)	0.26 ± 0.052	4.69	38
Flies (large)	0.04 ± 0.015	0.62	5
Chauliognathus pennsylvanicus	0.10 ± 0.035	1.85	15
Epicauta pennsylvanica	0.05 ± 0.020	0.86	7
Diabrotica longicornis	1.21 ± 0.153	21.73	176
Disonycha spp.	0.64 ± 0.087	11.36	93

in glycerol alcohol (70%). Due to the destructive nature of this sampling, six random (i.e. non-marked) single (flowering) ramet genets were collected in order to estimate stigma loss for the smaller clone sizes. These flowering heads were also used to describe and quantify the damage done by the early larval instars of the lepidopteran, Coleophora spp., a seed predator. Herbarium vouchers are in the University of Windsor Herbarium.

A few ramets from each of three different clones obtained on the campus of Iowa Lakeside Laboratory, Dickinson County, Iowa, were transplanted to 15 inch pots in a screened greenhouse area for floral phenology studies. Individual heads were tagged with thread and the sequence of flower opening within a head observed.

Seeds (achenes) were collected from October 29 to November 1,1979. Larger clones were harvested by running a north-south transect through the clone and collecting ramets within 20 cm of the tape. The entire inflorescence was removed, bagged and its position along the transect recorded. If the clone was too small or the density too sparse to harvest an ample number of ramets using the transect, distances (cm) of harvested ramets to the centre and periphery were recorded. This gave a satisfactory estimate of the ramet's position within the clone. The inflorescences were stored at 0°C until examined.

2. Laboratory Procedures

2.1 Pollinator Analysis

Each mounted insect specimen was examined under a dissecting microscope for presence, number, and location of pollen grains (Table 2). Fuchsin jelly mounts were made of this pollen in an effort to identify pollen types found on the body by comparison against field collected samples. This would enable me to detect any poly- or oligotropic pollinator movements. This is important in evaluating relative efficiencies of the visitors in the transfer of pollen. Unfortunately the simultaneously blooming species are all members of closely related tribes in the Compositae (see Table 3 for a list) and also have echinate (spiny) pollen that I could not distinguish under a light microscope (Skvarla, Turner, Patel and Tomb 1977).

2.2 Flower Analysis

To estimate the proportion of stigmas clipped per head, twenty heads from each ramet (n=27) were randomly chosen; 10 from the top portion of the infloresence and 5 from each of two side branches. The flowers in each head were sorted into flower type (ray or disc), and the number of each type clipped was counted. The early instar larvae of the seed predator, Coleophora were also censused. If a larva was encountered, size class (egg, small, medium or large instar), flower type (ray or disc), location of instar (ovary or corolla), and number of flowers destroyed were recorded.

Table 2. Location and amount of pollen on each insect visitor type.

VISITOR CLASS	POLLEN LOCATION	AMOUNT*	N
Epicauta pennsylvanica Meloidae	between eyes	C	19
	snout	S	
	combs on femur (1st pair of legs)	C	
Chauliognathus pennsylvanicus Cantharidae	between eyes	S	21
	base of metasternum	C	
	base of coxae (1,2)	S,C	
Diabrotica longicornis Chrysomelidae	none		22
	legs	L	3
Disonycha spp. Alticinae	none		13
Small Syrphids	thorax (underside)	S	8
	none		46
Medium Syrphids	thorax (underside)	S	2
	thorax "	C	12
Large Syrphids	thorax "	C	8
Wasps	thorax "	C	10
Bees	thorax "	C	5

* C=clump $\gg$100 grains
S=sparse 50-100 grains
L=light dusting $<$ 10 grains

Table 3. List of simultaneously blooming composite species. Nomenclature after Gleason and Cronquist 1963)

Tribe Astereae
Solidago rigida L.
S. missouriensis Nutt.
S. speciosa Nutt.
Aster ericoides L.
A. laevis L.
Tribe Heliantheae
Helianthus Maximiliana Schrader
H. grosseserratus Martens.
H. Rigidus (laetiflorus Pers.)
Tribe Eupatorieae
Liatris aspera Michx.
L. punctata Hook.

2.3 Seed Analysis

Seeds were stratified in the cold room at least two months before analysis. The number of heads sub-sampled per ramet reflected the size and condition (some seeds were beginning to disperse from the heads) of the inflorescence, since size variation was encountered between and within clones. From the majority of ramets however, fifteen heads per ramet were randomly chosen. These heads were examined under a dissecting microscope. The number of seeds per head was recorded and seeds were sorted into the following categories: normal seeds were classed as VIABLE; seeds that were only partially filled or were collasped with only a dried ovule inside were called NON-VIABLE; seeds that had been eaten by the Coleophora larva were classed as either VIABLE PREDATED or NON-VIABLE PREDATED. The remains of these seeds allowed accurate evaluation of class. To verify category placement VIABLE and NON-VIABLE seeds were weighed on a Cahn Automatic Electrobalance (Model 4700) to an accuracy of ±1 ug.

Viability was tested two ways. 1) In germination trials seeds were incubated in water overnight, rinsed in a 15% bleach solution and placed in small lockable petri dishes. The dishes were placed in a chamber set at 27°C with a 12 hour light/12 hour dark cycle. Germinations were checked daily. 2) In tetrazolium tests, the seeds were also incubated in water overnight, cut longitudinally to allow stain penetration and treated with a 0.5% solution of 2,3,5

triphenyl tetrazolium chloride (Sigma) (Moore 1973). The petri dishes were kept at room temperature (22°C) to minimize deterioration. Colourless tetrazolium reacts with the hydrogen released by tissue respiration, forming a water-insoluable red pigment, formazan and HCl. Seeds were checked for this red stain after 24 and 36 hours.

Partially-filled seeds and others that were questionable as to class assignment, were tested separately from the VIABLE and NON-VIABLE classes in the above tests. Based on the results of these tests, adjustments were made to class assignments.

RESULTS

1. Pollinator Results

Solidago's open, aggregated inflorescence and actinomorphic disc flowers make it accessible to most nectar and pollen gatherers, but nectar rewards are very small (0.0024 mg sugar/head; Heinrich 1976). The visitors can compensate for this low return by moving rapidly from head to head foraging without expending much energy. Pollen is constantly being renewed as new disc flowers open. When a foraging visitor moves over the heads, its legs and underside contact the "bottle brush" of pollen. Once deposited in these areas on the insect, further movement allows the pollen to contact any receptive stigmas. This primitive type of pollen transfer requires no coevolved pollinator behaviour and is called "mess and soil" pollination (Faegri and Van der Piji 1971).

Bumblebees (*Bombus* spp.) and honeybees (*Apis* spp.) are the usual pollinators of *Solidago* sp. (Heinrich 1976, Morse 1977, Werner et al. 1980), but on Cayler Prairie no bumblebees or honeybees were ever seen on *S. canadensis*. Other fall blooming species (Table 3), which offer greater nectar rewards, with the same ease of handling, attracted these pollinators (Werner et al. 1980). The main visitors of *S. canadensis* were syrphid flies, other flies, beetles, and a few solitary bees and wasps. Table 1 shows the mean number of visits per five minute observation period for

each visitor class and its overall importance expressed as a percentage of the total number of visits. It is not known if the visitor had been foraging on other ramets in the same clone, or if it had just arrived from another clone. The beetle visitors were observed visiting other fall blooming species. Small syrphid flies and the northern corn rootworm beetle, Diabrotica longicornis (Say.), are the most frequent visitors.

A quantitive examination of pollen loads on the body of each type of visitor (Table 2) reveals that the beetles, Epicauta pennsylvanica (DeG.) (blister beetle) and Chauliognathus pennsylvaicus (DeG.) (soldier beetle) along with the medium and large syrphid flies carry the most pollen. As mentioned, pollen types from the different composite species could not be distinguished from the pollen of S. canadensis, nor could self-pollen be separated from outcross-pollen. To assess the pollinating efficiency of the different visitors, Spearman rank correlation coefficients were calculated between the fertilization rate per head (from the seed data) and visitation frequency (Table 4). The main pollinator appears to be Chauliognathus pennsylvanicus. This agrees with the quantity and location of pollen found on the body. The correlation between fertilization rate and Diabrotica visitation frequency is also significant ($r=0.229$, $p=0.0057$). I believe the corn rootworm, Diabrotica, has a significant correlation with fertilization rate only

Table 4. Pollination efficiencies of each visitor class. See text for details. (N=145)

VISITOR CLASS	CORRELATION COEFFICIENT (rho)
Chauliognathus pennsylvanicus	0.25589 p = 0.0019*
Epicauta pennsylvanica	0.02730 p = 0.7445
Diabrotica longicornis	0.22874 p = 0.0057
Small Syrphids	0.08642 p = 0.3014
Medium Syrphids	0.02453 p = 0.7696
Large Syrphids	0.11931 p = 0.1529
Wasps	0.12014 p = 0.1500
Bees	-0.09078 p = 0.2775

* probability $>$ R under H_o:Rho=0.

because its numbers are correlated with Chauliognathus numbers (Spearman's rho=0.344, $p<0.0001$), since virtually no pollen was found on its body. A correlation may result because these two beetles overlap temporally in their exploitation of Solidago. By the presence of pollen on their bodies, one might expect both the medium and large syrphid flies and Epicauta to have significant correlations with the fertilization rate. Epicauta eats the stigmas of flowers as it forages for nectar and pollen, which would pre-empt any pollination. No correlation with fertilization rate would thus be expected. Indeed, Werner et al. (1980) found a negative correlation between the number of E. pennsyvanica individuals per ramet and seed set. The lack of pollination efficiency in the syrphid flies reflects their tendency to fly between ramets of the same clone, transferring largely self-pollen. However, the sample size (n=31) may be too small to detect a correlation.

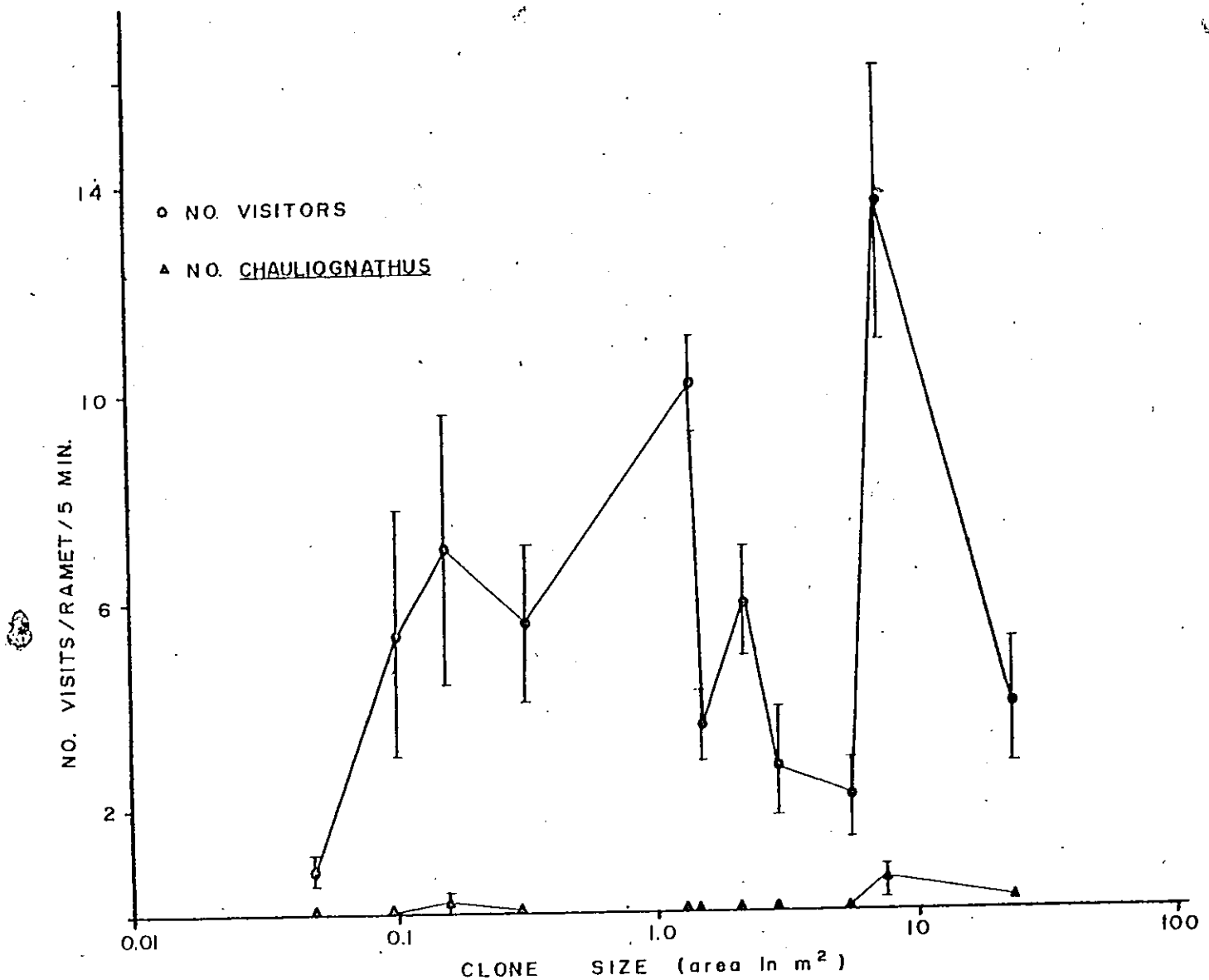
Observing only quantity of pollen carried by a visitor may be misleading. After foraging on a ramet and before departing, beetles preen their body of pollen and eat it. Chauliognathus, the soldier beetle, carries the majority of its pollen in harder to preen areas (e.g. base of the metasternum) than the blister beetle (e.g. snout), which will influence the total pollen available for pollination. Pollen located on the underside will contact receptive stigmatic surfaces more often while the insect is foraging.

The overall mean visitation frequency (all visitors combined) differs significantly among clones (Fig.3). Using a Kruskal-Wallis test (Conover 1971, Gibbons 1971), the chi-square approximation equals 61.41 (df=10, $p<0.0001$). Visitation frequency is positively correlated with clone size (Fig.3) (rho=0.2617, p=0.0015). Unfortunately, no differences among the clones could be detected in the mean visitation frequency of the soldier beetle, Chauliognathus (Kruskal-Wallis test, $x^2=9.88$, df=10, p=0.4510). This is due to the very low numbers recorded (n=15). Consequently many clones had zero entries. There is a significant correlation between the number of soldier beetle visits and clone size (rho=0.276, p=0.0008)(Fig.3), suggesting that an increase in patch size will lead to a corresponding increase in the numbers of Chauliognathus visits.

There are no differences in overall mean visitation frequency among positions (periphery, middle, center sections of clones) within a clone (Kruskal-Wallis test, $x^2=0.61$, df=2, p=0.7369), or in soldier beetle mean visitation frequency (Kruskal-Wallis test, $x^2=0.07$, df=2, p=0.9638). Also no correlation with position is apparent (overall visitor frequency, rho=-0.057, p=0.4969 and soldier beetle frequency, rho=-0.038, p=0.6496). Apparently the insects are treating each clone as a homogenous resource, regardless of size, and are not actually choosing specific areas within a clone.

Figure 3

The effect of clone size on the number of floral insect visitors. The mean number of flower visitors, and Chauliognathus, the major pollinator, per ramet in a five minute observation period, as a function of clone size expressed as an area in square metres. Bars indicate ±1 standard error (SEM).


o NO. VISITORS
▲ NO. CHAULIOGNATHUS
NO. VISITS/RAMET/5 MIN.
14
10
6
2
0.01
0.1
1.0
10
100
CLONE SIZE (area in m²)

The visitation frequency are based on five minute observation periods, and the very small visitor means reflect this. Even when expressed as the numbers of daily visits, there seems to be a paucity of visitors.

In the period when the visitor observations were carried out, the different clones were not all at the same flowering stage. If some (e.g. clone size=23.7) clones were past their peak, their attractiveness as a food source was diminished, resulting in a lower number of visitors in that period.

2. Flower Results

There are two distinct sources of flower predation in S. canadensis: 1) the consumption of ovaries and destruction of disc flower buds by the larva of the lepidopteran, Coleophora spp. (Coleophoridae) and 2) stigma clipping by the black blister beetle, Epicauta pennsylvanica.

2.1 Coleophora predation

Coleophora sp. is a seed-predator of Solidago spp., and its impact on viable seed output will be considered in a later section. In this section the damage done to the ovary and flower by the younger instars will be quantified.

The female Coleophora deposits single eggs on the pappus of the ray flowers as Solidago comes into bloom in mid-August. Usually only one egg is laid per head. Once hatched the larva crawls down into the head and eats the

immature ovaries, leaving a characteristic frass in the head. The older instar larvae locate a disc flower bud and enter it by chewing a hole at the base of the corolla. They orient their heads toward the ovaries. The predated disc buds subsequently turn brown and remain closed. Pollen could be another possible food source, since the anthers still release pollen. This sequence of events is synchronous with the pollination process.

The larva starts to form its characteristic case by cementing the pappuses and corollas of several flowers together with silk and excrement (McDunnough 1956). The case is a slender tapered tube with a three valved apex. The larva's head and upper thorax protrude from the open end, enabling it to crawl. There are two lines of evidence which suggest the larva is very mobile and moves to other heads once it has destroyed part or all of its original head. The first line of evidence is that there are more heads with no predation (81.2 percent not predated) at this earlier stage than once predation has terminated with onset of seed production (66.69 percent not predated in the seed data). Secondly, the mean percent flower predation per head is 6.27 ± 0.784. Correcting for ten of 500 heads that were totally predated, a class which would not be observed once the seed has set, the mean percent flower predation is only 4.36 ± 0.515. At the time of seed set the non-viable predation rose to 6.65 ± 0.359 percent per head. The increase in these two gauges of intensity over time,

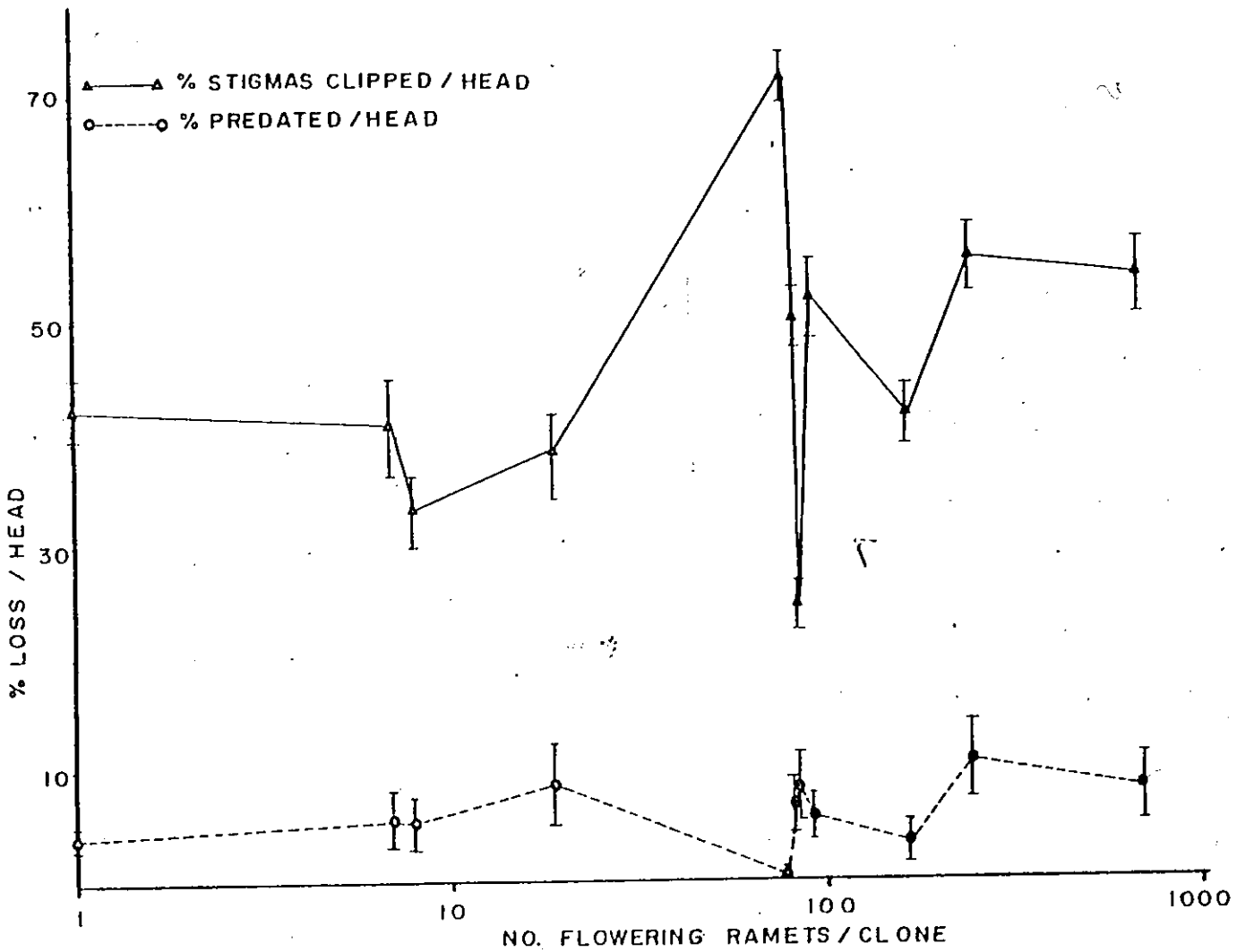
implies mutliple head destruction by individual larva as they mature.

When pollination and fertilization are complete, the larva is fully mature and consumes viable seed. Its thin parchment-like larval cases are easily seen protruding out of the head. There are no direct counts of how many heads the younger instars consume before they form their cases, nor how many heads of viable seed the older "case-bearers" utilize. In the late fall (October-November) the larva caps its case and falls to the ground where it pupates in the spring (Borror and DeLong 1971).

In light of Root's (1973) "resource concentration hypothesis" a question may be asked: Since clones are "monocultures" of resource, does the female Coleophora differentiate between clone sizes or total number of flowering ramets per clone? There are no differences in the mean predation rate among clones (Kruskal-Wallis test, $x^2=3.88$, df=10, p=0.9526), nor is there any trend with clone size (Spearman's rho=0.0007, p=0.9877) or its associated number of flowering ramets (rho=0.01995, p=0.6563). Overall, the percent predation per head is very low in all clones (Fig. 4), and the variation within clones is very high (i.e. standard errors are large). This combination may contribute to the lack of clone size effects. In addition neither the damage per larva, nor the number of larvae per ramet examined is known. The number of ramets sampled per clone is small (1-3/clone), which may

Figure 4

The effect of clone size on floral predation. The mean percentage of stigmas clipped per head and flowers predated per head plotted against the number of flowering ramets per clone. Coleophora sp. consumes the flower's ovule, and Epicauta sp. clips and eats the stigmas. Bars indicate ±1 SEM.


% STIGMAS CLIPPED / HEAD
% PREDATED / HEAD
70
50
30
10
% LOSS / HEAD
1
10
100
1000
NO. FLOWERING RAMETS / CLONE

underestimate the damage. Indeed, when analyzing the final mean percentage of ovules predated, using the seed data, there are significant differences among clone sizes, larger clones experiencing more predation (see Section 3.2).

It is interesting to note that of the five single ramet genets sampled, three had no predation at all, one had very low predation (mean % predation=1.25±1.25), but one had 16.7±2.50 percent predation which was confined to disc bud destruction. So the single ramet genets are almost as variable (Coefficient of Variation=239.1, n=100) as all the other clone sizes combined (CV=274.8, n=400).

Once in a clone, does the female Coleophora select ramets by region? There are no differences in mean percent predation among positions (peripheral, middle or centre) (Kruskal-Wallis test, x^2=1.09, df=2, p=0.5805) and no trend with position (rho=-0.036, p=0.4212). This may indicate that the female Coleophora does not select any particular location, but perceives the clone as a homogenous resource.

Once a ramet has been chosen, is there any preference for an area (top or sides) within the inflorescence? There is no difference between the areas (Kruskal-Wallis test, x^2 =0.59, df=1, p=0.4425). It appears that the ramet is a homogenous patch within a patch.

Since the disc flowers attract the pollinators by providing the "attractants", pollen and nectar, it would be instructive to partition the total floral predation into percentage of disc and ray flowers predated. The

contribution of flower type to seed formation can then be determined. The number of rays (mean=10.68±0.089) is always larger than the number of discs (mean=4.57±0.057) within a head. To make them comparable, the predation in each class (ray or disc) is divided by the corresponding number of ray or disc flowers. The disc flowers are predated, on a percentage basis, more than the ray flowers (Student's $t=6.71$, $p<0.0001$), with the mean predation per head of 11.14±1.227% and 4.2±0.747%, respectively. Thus the number of ray ovaries eaten per head is small (0.042x10.68=0.4486 ray/head). In the disc flowers however, not only is the female part (i.e. ovary) destroyed, but the male portion (pollen) is also destroyed, limiting the pollen available for pollination. An average of half a disc flower (0.114x4.57=0.509) is destroyed in each head of the whole ramet by the Coleophora larvae.

2.2 Epicauta Stigma Predation

Epicauta visits Solidago, like many insects, to collect pollen and nectar. However, its impact on seed-set is more serious than those insects that only steal pollen, without affecting pollination. It clips the stigmas and eats them, pre-empting the flower from possible fertilization, and consequently wasting the ovule. Expressed as a percentage of the flowers per head, the mean is 44.87±1.071% clipped.

There were only seven Epicauta pennsylvanica recorded

in the pollinator census, therefore it is not surprising no difference among clones could be found in mean visitation frequency (Kruskal-Wallis test, $x^2=0.96$, df=10, p=0.9999). There are however, significant differences among clones (or flowering ramet number) in the mean percentage of stigmas clipped per head (Kruskal-Wallis test, $x^2=108.8$, df=10, $p<0.0001$). Because there does not seem to be a direct relationship between the cause (number of Epicauta cencused) and the effect (percent of stigmas clipped) may reflect the voracious consumption by individual beetles. With increasing number of flowering ramets per clone, the percent clipping increases (rho=0.1705, $p<0.0001$), but the clone to clone variability is great (Fig.4). Again variation between single ramet genets is large; the percentage clipped per head ranges from 17.67 to 72.32. The coefficient of variation is larger (CV=67.25, n=100) among single ramet genets than among all the other clone sizes combined (CV=49.85, n=400).

Is the clipping damage concentrated in any specific area of the clone? If the clones with only one position analyzed are removed, so sample sizes for each position are similar, the positions (i.e. ramets located in the periphery, middle and centre of the clone) differ significantly from each other in the mean clipping rate (Kruskal-Wallis test, $x^2=8.78$, df=2, p=0.0124). The amount of clipping increases from periphery to centre of a clone (rho=0.221, $p<0.0001$, all clones considered; rho=0.155,

$p=0.0056$, clones with more than one position analyzed) (Fig.5), but the relationship is not apparent in each individual clone.

Any preference for flower type by Epicauta can be evaluated by splitting the total percentage clipped per head into its constituents, ray or disc flowers. Biologically, since the disc flowers produce the pollen and nectar, one might expect them to have a higher probability of being clipped. Again, each percent is expressed as a function of the number of either disc or ray flowers per head. The mean percentage clipping per head is 68.77 ± 1.419 for disc flowers and 34.52 ± 1.218 for the ray flowers. The flower types differ significantly ($t=-22.53$, $p<0.0001$) in the amount of clipping suffered (Fig.6). Like Coleophora, Epicauta preferentially selects disc flowers. Expressing these losses in number destroyed per head, 3.67 (10.68x0.345) ray and 3.14 (4.57x0.688) disc flowers are clipped, on average, from each head.

2.3 Total Predation

The total impact on each flower type can be compared by summing the two sources of destruction and expressing this as a function of the number of either ray or disc flowers affected per head. The total percent disc flower destruction is 79.9 ± 1.435, while in ray flowers it is 38.72 ± 1.405. Of the total 10.68 ray flowers per head, an average of 6.55 will be left functional for fertilization, compared

Figure 5

The effect of clonal position on the percentage of stigmas clipped per head. The mean percentage of stigmas clipped per head as a function of position (peripheral, middle or centre) of the ramet within a clone. The number adjacent to each curve represents the number of flowering ramets in that clone. No clones with only one position sampled are plotted. Bars indicate ±1 SEM.

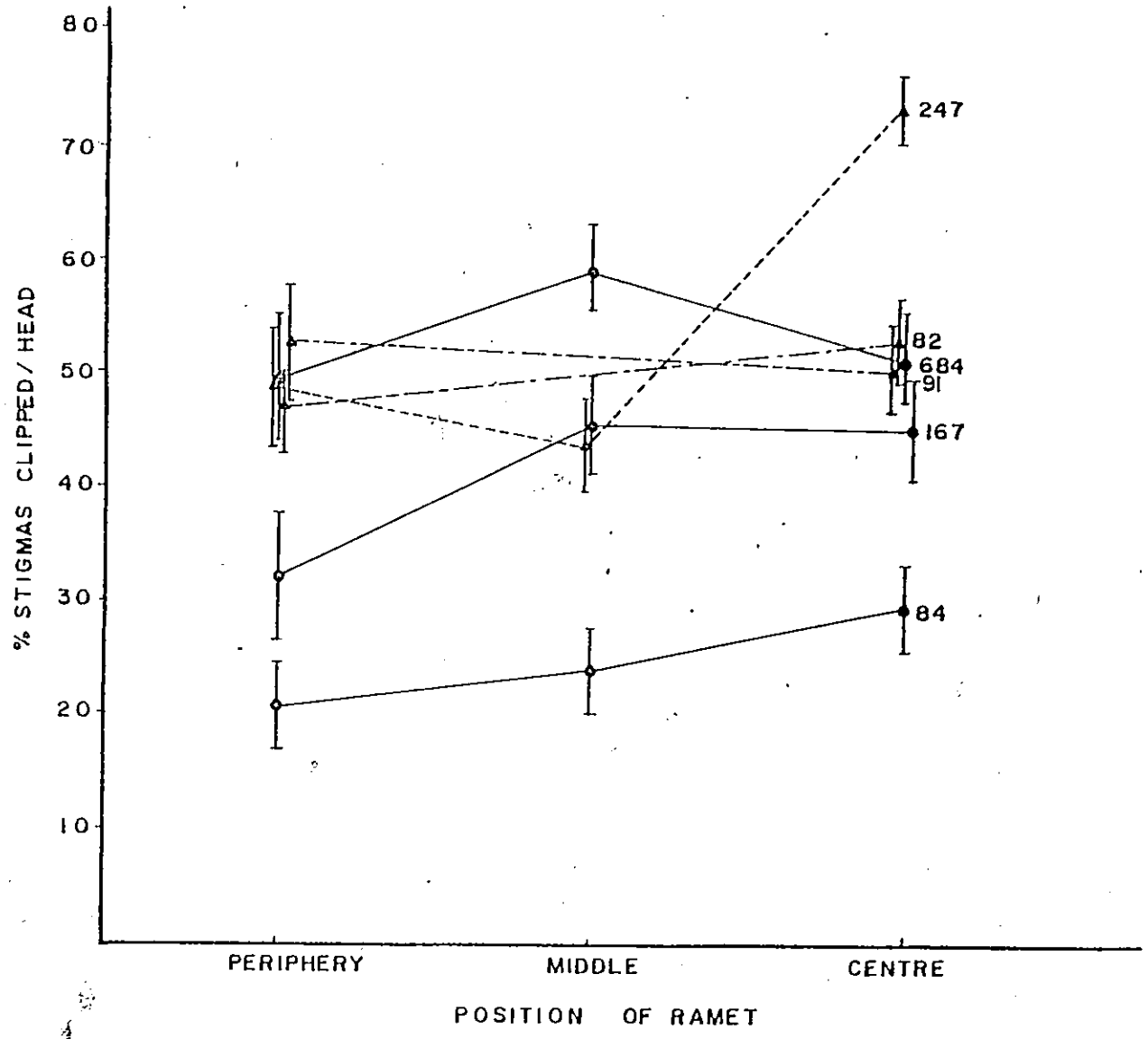
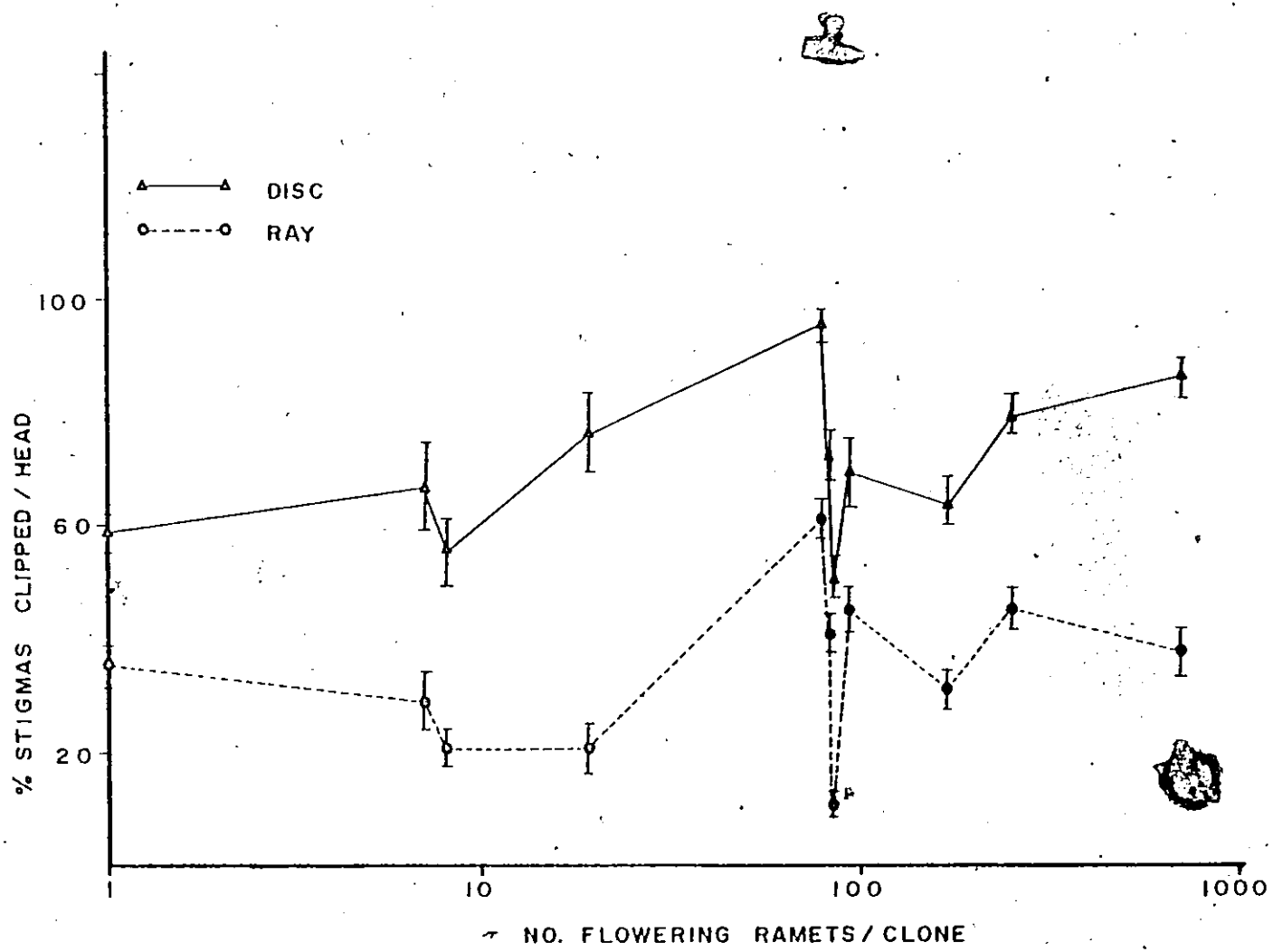

80
70
60
50
40
30
20
10
% STIGMAS CLIPPED/HEAD
247
82
684
91
167
84
PERIPHERY
MIDDLE
CENTRE
POSITION OF RAMET

Figure 6

Comparison of the mean percentage of ray and disc stigmas clipped per head as a function of the number of flowering ramets per clone. Bars indicate ±1 SEM.


DISC
RAY
100
60
20
% STIGMAS CLIPPED / HEAD
1
10
100
1000
NO. FLOWERING RAMETS / CLONE

to only an average of 0.92 of the 4.57 disc flowers per head. It is obvious most of the seeds set will be derived from ray rather than disc flowers.

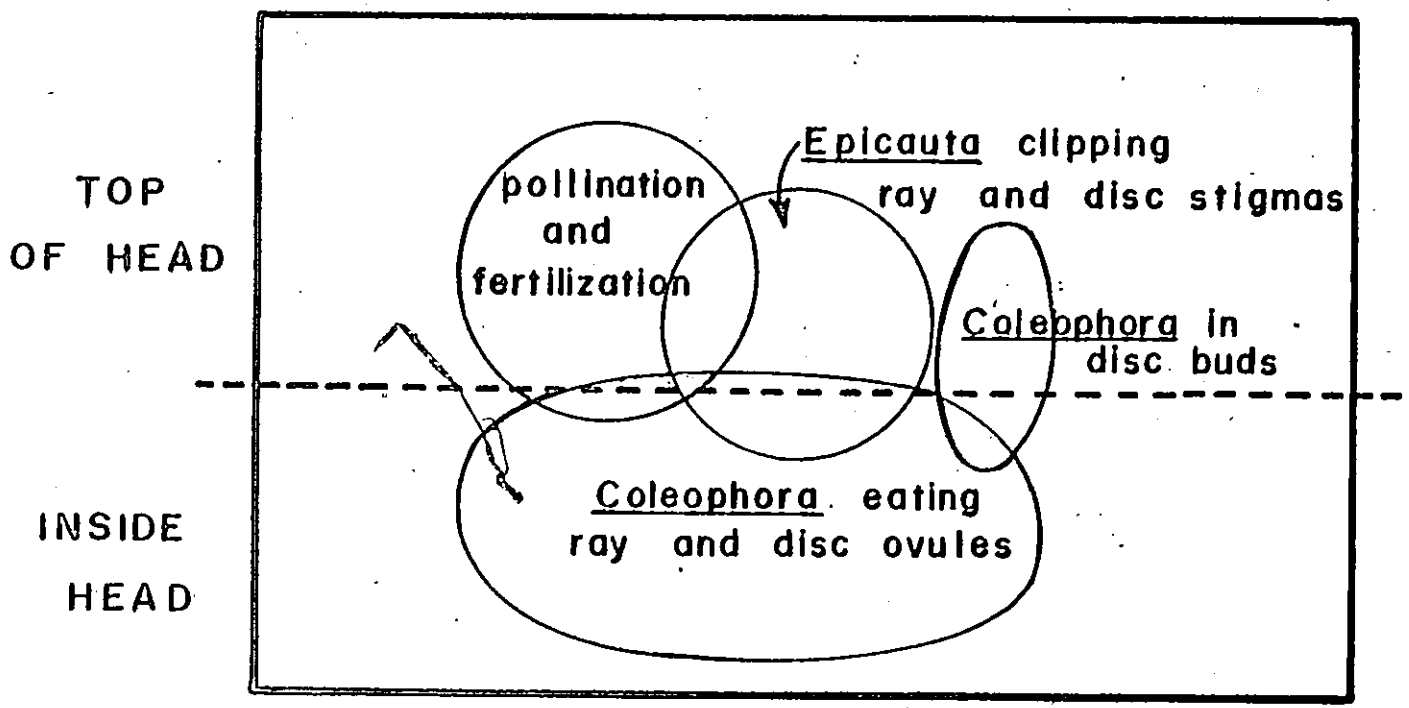
The processes of pollination, fertilization, stigma clipping and ovule predation can not be temporally separated. They are occuring at the same time, at different sites within a head. Since these functions are concurrent, the mean total predation may be inflated. Figure 7 shows how this might happen. An Epicauta might clip the stigma of a flower that has already had its ovule eaten by a Coleophora larva. Therefore only one flower has been affected but it would be counted as two in the calculations. If a Coleophora larva destroyed a disc flower bud, it is unavailable for clipping, since it never opens. Even if that bud's ovule had already been destroyed, it would still only count as one predated flower. This decreases the possible over-estimation in disc flower predation. Thus, the mean total predation may be inflated for ray flowers but it is probably close to real for the disc flower.

3. Seed Results

The information obtained from the seed analysis will be presented in three sections: 1) Factors affecting the total number of flowers fertilized per head, regardless of fate, 2) seed predation, and 3) the resultant seed output.

Figure 7

Venn diagram illustrating the temporal overlap in the different functions within the head.


TOP
OF HEAD
INSIDE
HEAD
pollination
and
fertilization
Epicauta clipping
ray and disc stigmas
Coleophora in
disc buds
Coleophora eating
ray and disc ovules

3.1 Flowers Fertilized per Head

This section considers the contribution of a number of variables to the pattern of flower fertilization over a range of clone sizes. Since it is energetically less costly for an insect to fly between two ramets within a clone than between clones, one might expect an increase in inter-ramet pollinator flights as clone size increases. Ramets of a clone are genetically identical, so any intra-clonal transfer of pollen will not result in viable seed production. The total number of fertilized flowers consists of those producing viable seed, those that had been fertilized but were later consumed by Coleophora (VIABLE PREDATED), and those producing "partially filled" seed that had been fertilized but had for some unknown reason aborted. Since the total number of flowers per head varies between heads within a ramet and between ramets, the fertilization index is expressed as a function of the number of flowers per head. The overall mean percentage fertilized per head is 25.26± 0.481, and ranges from 0 to 82.35.

The variance of a proportion (or percentage) equals p(1-p), where p is the proportion, and thus varies with p (Cohen and Cohen 1975). To correct for these unequal variances, the proportions were arcsine transformed (2arcsine $\sqrt{p}$). There are many zero values in the data which were transformed using the correction factor

p=1/(4xn) (total n=1414 heads) (Owen 1962). This makes them non-zero, but maintains their relationship to the other entries. Once transformed the variances are homoscedastic between clones (F max=3.27, $p<0.05$ (Sokal and Rohlf 1969)).

The clonal habit of S. canadensis necessitated a nested design, since heads are nested within ramets and ramets are nested within clones. This type of design enabled me to assess the following sources of variation at each level: the differences between clones, the differences between ramets within a clone and the errror term, head to head variation within ramets. The clonal differences were specified in the analysis by using "clone", which is a dummy variable, i.e strictly qualitative. Each ramet was nested in its appropriate clone by specifying "position within clone" (i.e. position(clone)). By specifying "clone" in the model, all possible clonal differences are accounted for. Any specific variable that contributes to overall differences between clones is a co-variate, and as such is removed from the term "clone", and not the error term. The same applies to any variable that differs between ramets within a clone. Any positional (i.e. ramet) differences will be partitioned from the "position(clone)" term. Due to the complete confounding of the variables within their appropriate nest level, the co-variates are entered before the terms "clone and position(clone)" (GLM Procedure, SAS 1979, Barr, Goodnight,

Sall, Blair and Chilko 1979).

Many of the co-variates are correlated, and as such are not orthogonal. This influenced the selection and order of the co-variates in the model. Table 5 is the correlation matrix of all measured variables.

The whole suite of possible clonal parameters shown (Table 5) was not used in the model, since biologically some are more reasonable than others. Since this study dealt with flower pollinators and predators, it is more logical to use the total number of flowering ramets per clone than total number of ramets per clone or clone size. The number of flowering ramets better defines the size of the resource patch and is probably the initial unit of perception for any insect visitor. Due to the high inter-correlations among variables, once the number of flowering ramets is entered, the total number of ramets and clone size explain no additional signigicant variation in fertilization rate. Their extreme multicollinearity could also invalidate the model. This is another reason to enter only one of the mentioned variables (Nie, Hull, Jenkins, Steinbrenner and Brent 1975). The total flowering mass may not be the only aspect of the clone an insect perceives; the density of the flowering ramets may contribute to the overall attractiveness of the clone. Two measures were considered: 1) the number of flowering ramets per square metre, and 2) the distance (cm) to the nearest flowering ramet. Both measures assume ramets within a clone are

Table 5. Pearson Correlation Matrix for the Arcsine Transformed Percent Fertilized/head and all independent variables. (n=1414) $p < 0.0001$ unless otherwise specified.

	Arct	Flno	No	Clsz	Pclip	Ppred	#clone	Near	Flnnd	Tnnd	Dist	Hdtot	Ramm
Flno	0.367												
No	0.336	0.958											
Clsz	0.386	0.978	0.970										
Pclip	-0.139	0.326	0.295	0.197									
Ppred	0.178	0.398	0.343	0.354	-0.107								
#clone	0.132	0.083 .002	0.194	0.135	-0.432	0.382							
Near	-0.179	-0.207	-0.229	-0.195	-0.070 .008	-0.153	-0.271						
Flnnd	0.132	0.292	0.485	0.415	-0.264	0.098 .0002	0.432	-0.096 .0003					
Tnnd	0.281	0.643	0.699	0.707	-0.064 .017	0.224	0.139	-0.145	0.801				
Dist	-0.092 .0005	0.082 .002	0.093 .0004	0.077 .004	0.218	-0.025 .358	0.079 .003	-0.150	0.216	0.243			
Hdtot	-0.05 .062	-0.177	-0.082 .002	-0.121	0.029 .281	-0.381	-0.346	-0.057 .034	0.194	0.140	-0.005 .847		
Ramm	-0.385	-0.41	-0.378	-0.486	0.293	-0.154	-0.087 .001	0.440	-0.172	-0.298	0.037 .168	-0.089 .0008	
Flramm	-0.198	-0.181	-0.319	-0.337	0.302	0.114	-0.191	0.208	-0.365	-0.130	0.111	-0.235	0.704

Arct=Arcsine Transformed Fertilization'Percent/head;Flno=#flowering ramets/clone;No=#ramets/clone;Clsz=Clone size(m^2);Pclip=Percent clipped/head;Ppred=Percent floral predation/head;#clone=#clones in 5 m; Near=Distance to nearest clone;Flnnd=Distance to nearest flowering ramet in clone; Tnnd=Distance to nearest ramet in clone;Dist=Distance from periphery of clone;Hdtot=#flowers/head;Ramm=#ramets/m^2; Flramm=#flowering ramets/m^2.

equidistant. Although the analogous measurements on the total number of ramets (the number of ramets per square metre and the distance to the nearest neighbour), have higher correlations with the seed set, their higher correlations with number of flowering ramets preclude their inclusion in the analysis. Their effects are accounted for by their floral variable counterparts, to which they are highly correlated.

The Maximum R^2 improvement technique of Stepwise Regression (Stepwise Procedure, SAS 1979, Barr et al. 1979) was used to select the optimal model and order. After each new variable is added, all possible switches are considered to see if removing one variable and replacing it with another not yet entered would increase R^2. This switching aspect is important since many of the independent variables are correlated.

The final model used is shown in Table 6. The total model explains 46.4% of the variation in fertilization rate and subsequent seed-set. Of that, the co-variates considered explain half, 23.48%. The error term, which accounts for more than 50% of the variation, reflects the large head to head differences within individual ramets. The following sub-sections examine each co-variate in the model.

3.11 Number of flowering ramets per clone.

This variable accounts for over half of the total difference between clones (46.622 of the possible 84.836

Table 6. Nested Anova for the arcsine transformed percentage fertilized/head.

SOURCE	DF	SUM OF SQUARES	MEAN SQUARE	F VALUE	PR > F	R^2	CVZ
Model	123	160.42791637	1.30429200	9.08	0.0001	0.46404	39.006
Error	1290	185.29539101	0.14363984				
Corrected Total	1413	345.72330738					

SOURCE	DF	TYPE I SS	F VALUE	PR > F
Number of flowering ramets/clone	1	46.62188331	324.57	0.0001
Percentage of stigmas clipped/head	1	25.98348302	180.89	0.0001
Distance to nearest S. canadensis clone	1	3.91369909	27.25	0.0001
Distance to nearest flowering ramet within the clone	1	3.12966976	21.79	0.0001
Percentage floral predation/head	1	1.51381697	10.54	0.0012
CLONE	15	8.40204237	3.90	0.0001
POSITION(CLONE)	103	70.86332184	4.79	0.0001

Sum of Squares, Appendix 2), and hence is the most important of the co-variates considered. As a clonal parameter, that is, a variable indigenous to each clone, its effect is partitioned from the term "clone". Figure 8 shows the increase in percentage seed set per head as the number of flowering ramets increases. This indicates that on the average the number of viable pollinations does not decrease, as has been predicted, with the flowering ramet number. It would seem that inter-ramet intra-clonal flights by the pollinators are not increasing enough to preclude successful pollination.

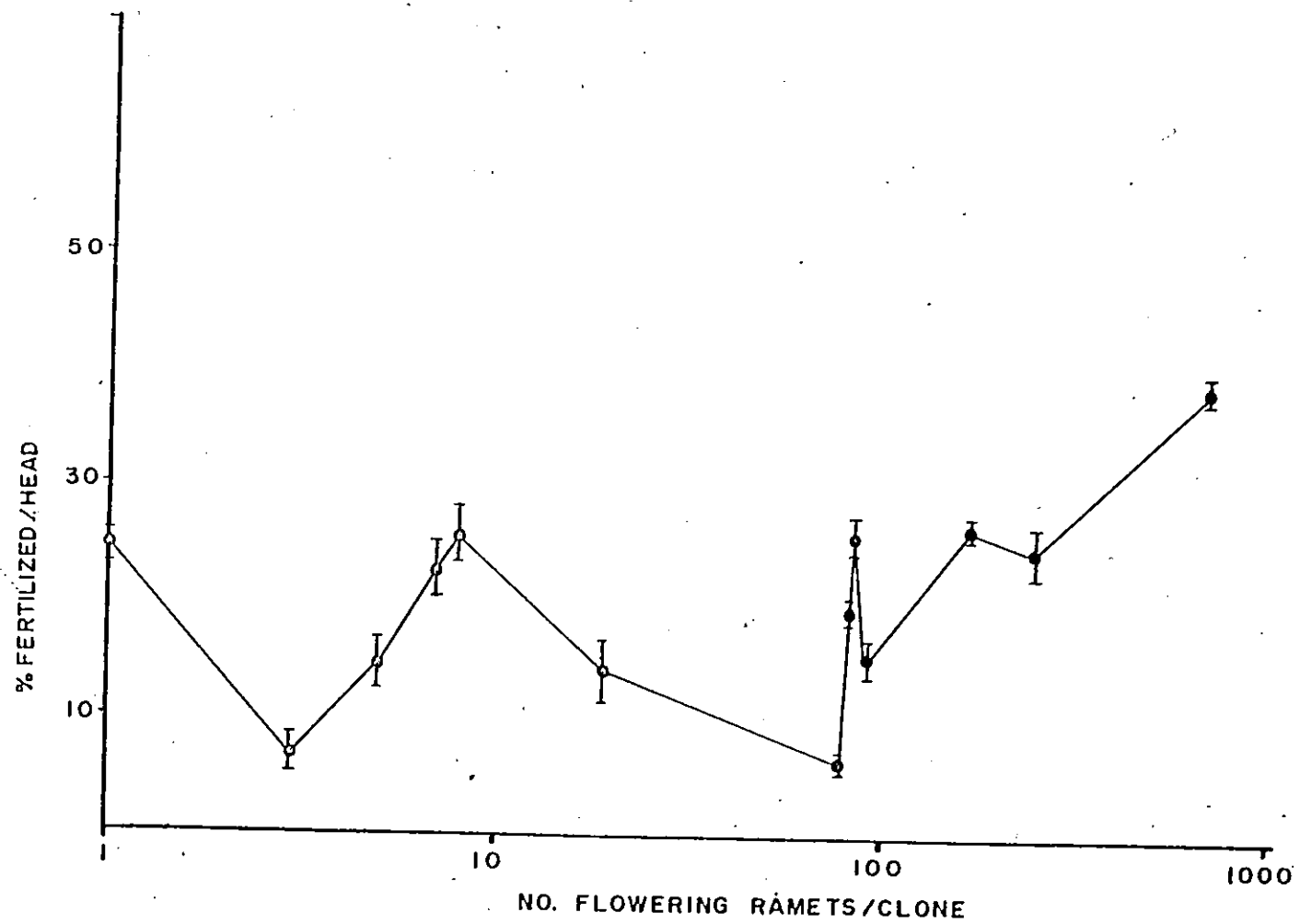
3.12 Percentage of stigmas clipped per head.

The percentage of stigmas clipped per head becomes an important variable in determining the amount of seed-set. The removal of stigmas pre-empts fertilzation and places a defined ceiling on possible seed-set, regardless of pollinator dynamics. This partially explains the variation around the trend of increasing seed-set with increase in the number of flowering ramets. In particular, the clone whose flowering number is 78 (Fig.8), has a much lower seed-set than other clones in that same size catagory. The reason is that it has a mean clipping rate of over 71% (Fig.4).

Measurement of the percentage of flowers clipped and/or predated per head results from destructive sampling. Therefore only the mean per location (peripheral ,middle, and centre) is used in this model. Each head sampled in

Figure 8

The effect of clone size on seed-set. The mean percentage of flowers fertilized per head as a function of the number of flowering ramets per clone. Bars indicate ±1 SEM.


50
30
10
% FERTILIZED/HEAD
1
10
100
1000
NO. FLOWERING RAMETS/CLONE

the seed analysis does not have a direct evaluation of the number of clipped stigmas or ovules predated. Each ramet was placed into its appropriate location, depending on position in the clone and the mean for that ramet used as an estimate. Therefore the model does not include any within-ramet variation for these two variables. As a result, their correlations with the number of flowering ramets are much inflated (see Section 2.2). The correlation of percent clipped in the original data, with the number of flowering ramets is low (rho=0.1705, $p<0.0001$), with much clone to clone variation.

As mentioned previously temporal overlap in stigma clipping, flower predation and fertilization may lead to inflated estimates of floral predation. Epicauta may also eat a stigma that has already been fertilized (Fig.7). This is not an important bias since only a few ovaries with clipped stigmas looked inflated enough to have been fertilized.

Significant differences were found in the percentage stigmas clipped per head as a function of 1) number of flowering ramets/clone, and 2) their position within the clone (see Section 2.2). The analysis reflects this two level effect by partitioning the clipping rate from both the "clone" and "position(clone)" term. The difference between clones represents 21.749 of the total 25.984 Sum of Squares due to clipping, while the differences between ramets within a clone account for 4.234 (Appendix 3).

Effects can be partitioned in this fashion by adding each co-variate sequentially into the model, and partitioning the Sum of Squares removed from the appropriate nested variable. So although the majority of the clipping effect on seed-set is at the clonal level, subtle differences are apparent within clones as well.

3.13 Distance to the nearest Solidago canadensis clone.

In such a heterogenous community, pollen flow may be influenced by a clone's neighbours. The relative isolation of each clone was indexed by 1)counting the number of S. canadensis clones within a five metre radius of the periphery and 2)measuring distance (cm) to the nearest flowering S. canadensis clone. It may be that an insect first peceives the overall floral density of the neighbourhood, and then cues in on a clone. The positive correlation (Pearson's Correlation Coefficient $r=0.1316$, $p<0.0001$) of seed-set with number of clones in a five metre neighbourhood, loosely suggests this. This trend is complicated by the negative correlation ($r=-0.432$, $p<0.0001$) between the number of clones in a five metre radius and the percentage of stigmas clipped per head. Again since the clipping rate is a mean value the true correlation is smaller ($rho=-0.278$, $p<0.0001$). Also the closer a neighbouring clone is, the higher the seed-set ($r=-0.1792$, $p<0.0001$). The inter-correlations between these factors make their effects upon seed-set difficult to assess. The true contribution of these two variables

cannot be evaluated because the quality of the neighbouring clones was not assessed (e.g. size of clone, number of flowering ramets, actual pollen flow between the clones or flowering stage). In larger clones the pollen flow may be very localized, directly affecting only those ramets in the immediate area. This was also not assessed.

Only the distance (cm) to the nearest clone enters into the model, because the number of S. canadensis clones in five metres is highly correlated with percentage of stigmas clipped, which is already in the model. As a clonal descriptor, its effect is partitioned from the "clone" term (Table 6).

3.14 Ramet density within clones.

Of the two different but equivalent measures of density, the number of flowering ramets per square metre and distance to the nearest flowering ramet, the latter enters the model because of its smaller correlation with the distance to nearest S. canadensis clone, which has already entered the model. Both of these density measures are estimates derived from the number of flowering ramets and the area occupied by the entire clone, rather than actual measurements.

The effects of density on seed-set may be divided into two categories. First, the overall floral density may be another cueing factor in attracting insect visitors to the clone. Secondly, once a clone has been selected, densely packed flowering ramets could influence the rate of

inter-ramet visits by the insects. If the next ramet is closer, pollinators may be more likely to visit another ramet in that clone and hence decrease fertilizations. Although there is a signigicant positive correlation ($r=0.1322$, $p<0.0001$) between seed-set and distance to the nearest flowering ramet, Figure 9 illustrates that the trend is not one of smooth increase. The true relationship is obscured because the percentage of stigmas clipped per head has a negative correlation ($r=-0.2643$, $p<0.0001$) with distance to nearest flowering ramet. If both ramet to ramet visits and the percentage of stigmas clipped decreased as distance between ramets increased (i.e. density decreased), I would expect a larger increase in seed-set than observed here (Fig.10). It appears that density does not greatly influence the within-clone dynamics of pollinator foraging. It indirectly suggests there is no marked increase in inter-ramet visits indicated by seed-set, as a function of density. The observed effects may also indicate that the distances between ramets (10-30 cm) is too small to make any difference to pollinators.

Density, expressed as the distance to the nearest flowering ramet, explains a significant proportion of variation in seed-set, in addition to the contribution made by the size of the resource patch (number of flowering ramets/clone). Since ramet density did not seem to influence pollinator flights within the clone, the

Figure 9

The effect of clonal inter-ramet density on seed-set. The mean percentage of flowers fertilized per head as a function of distance (cm) to the nearest flowering ramet within the clone. The genets with only one flowering ramet are all represented at zero centimeters. Bars indicate ±1 SEM.

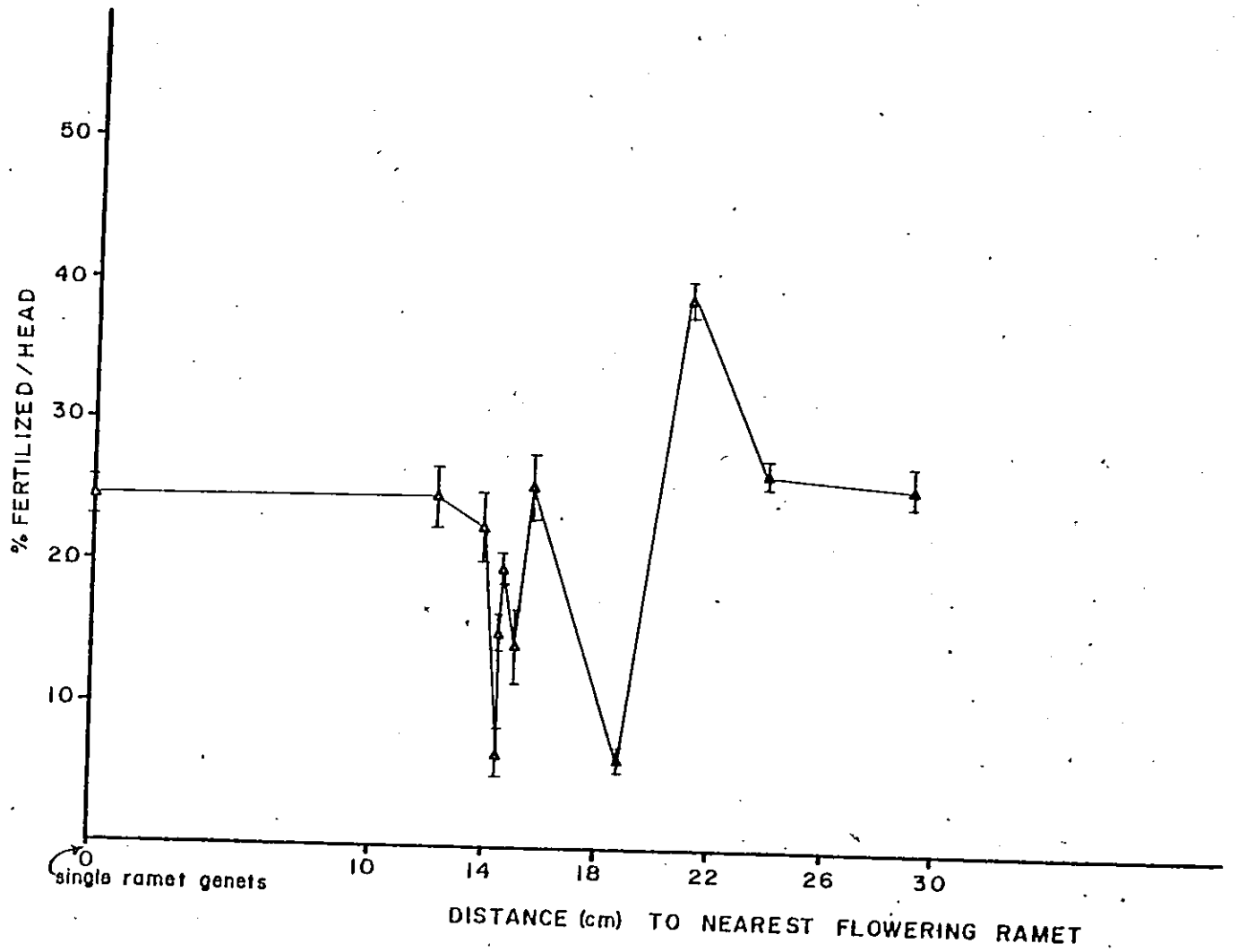
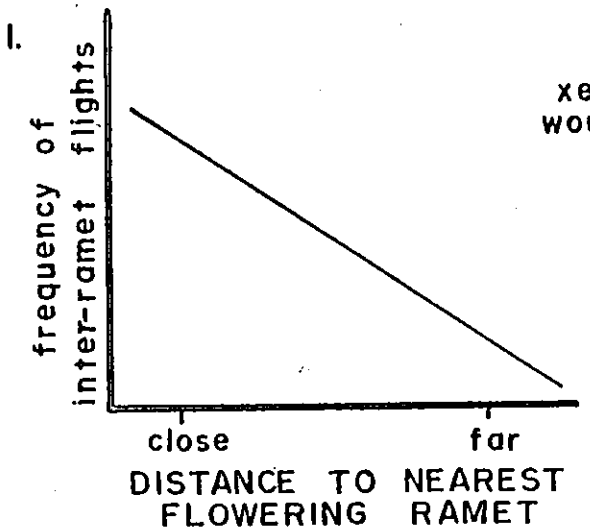

% FERTILIZED / HEAD
50
40
30
20
10
0
single ramet genets
10
14
18
22
26
30
DISTANCE (cm) TO NEAREST FLOWERING RAMET

Figure 10

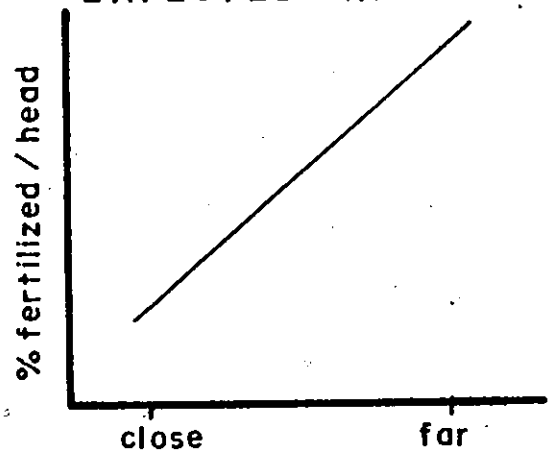
Expected outcome of increased intra-clonal density on the frequency of inter-ramet pollinator flights and seed-set. See text for details.

1.

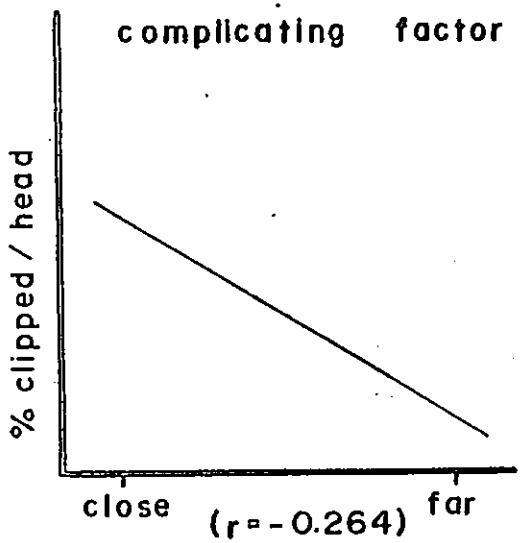


xenogamy would lead to:

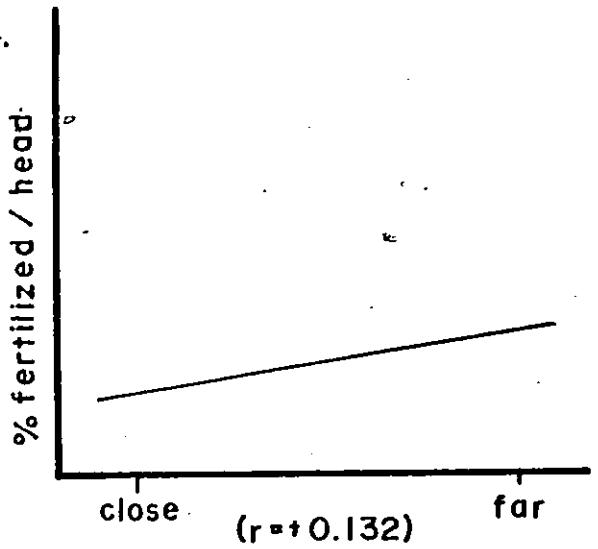
2. EXPECTED RESULT



3. complicating factor



4. FINAL RESULT



importance of density is probably in attracting pollinators to the clone. The entire effect of density is partitioned from the "clone" term, since the variable is homogenous over the whole clone (Table 6).

3.15 Floral predation per head.

The last co-variate considered is the percentage floral predation per head. In the Section 2.1 no significant differences could be found in this variable as a function of 1) the number of flowering ramets per clone and 2) position within a clone. This was partly due to the small sample size, but of greater importance is the large variation within each clone (Fig.4). As with percentage clipped, the predation estimate in analyzing seed-set is the mean for each location, which eliminates the large within clone variation.

The positive correlation of floral predation with seed-set is puzzling ($r=0.1776$, $p<0.0001$). Perhaps pollinators are attracted by the larval cases. More probably it is a result of the negative correlation between the percentage clipped and predation ($r=-0.1065$). This point will be expanded in the discussion of predation. The total Sum of Squares explained by floral predation is 1.514, of which 1.019 is partitioned from "clone" and 0.495 from "position(clone)" (Table 6). Even this small predation cost is important in determining seed-set.

In summary, the differences between clones significant in the model are: 1) the number of flowering ramets per

clone, 2) the percentage of stigmas clipped per head, 3) the distance to the nearest S. canadensis clone, 4) the distance to the nearest flowering ramet, and 5) the percentage floral predation per head. In the next level of the nest, differences between ramets (positions) within a clone, the percentages of stigmas clipped and flowers predated per head were found to contribute to the overall pattern of seed-set.

These co-variates only account for 23.48% of the possible 46.4% that are accounted for by clone and position differences. The clonal parameters partitioned a total of 76.434 from the total "clone" Sum of Squares of 84.836, leaving only 8.402 unaccounted. Most of the clonal differences have been quantified, without considering any microhabitat parameters. On the other hand only 4.729 of the possible 75.592 Sum of Squares for the difference between ramets have been accounted for. Most of the variation between ramets has not been quantified.

An examination of the residuals is important in evaluating the validity of any fitted model, regression or analysis of variance (Draper and Smith 1966). The residuals of this model indicate the model is adequate. The mean of the residuals is not significantly different from zero. The plot of residuals vs predicted values ($\hat{Y}$) indicates no gross abnormalities, since they appear in a "horizonal band" around the zero residual marker (Draper and Smith 1966). A normal probability plot of the

residuals shows that the model fits the mid-values better than the extremes (due to the many zero values). Also any model involving co-variables assumes equal slopes for each level of the co-variate (e.g. position). The slopes of percentage of stigmas clipped and flower predation per head for each level of position were tested and were found to be homogenous (GLM Procedure, SAS 1979, Barr et al. 1979).

Now several other variables not included in the final model will be considered.

3.16 Ramet distance from the clone periphery.

Such large differences between individual ramets within a clone were not expected. To evaluate the effect of location within a clone on seed-set, the ramets were ordered by their distance from the periphery of the clone. This was done by dividing the ramets' position by the radius of the clone, so these distances could be comparable across clone sizes. First the distance variable was regressed (GLM Procedure, SAS 1979, Barr et al. 1979) against the arcsine (to correct for unequal variances) of the seed-set for each individual clone. This tested if there was a linear trend in pollinator foraging from the outside to inside of a clone. Only the three clones with the greatest number of flowering ramets (167,247,684) had significant regressions. Their slopes are negative, indicating a decrease in seed-set from the periphery to centre of the clone. The slopes are very flat, and the R^2 are very low which indicates that even though the

regressions are significant, the predictive power of the regression is minimal. This variable is therefore less important in determining seed-set.

If distance from the periphery is entered in the overall model its effect is significant, but only because the clones for which this relationship is significant have the largest sample sizes and as such dominate the effect. For this reason distance of a ramet from the clone's periphery was omitted from the model.

3.17 Number of flowers per head.

The number of flowers per head ranges from 8 to 24, with a mean of 15.96 ± 0.07998. The fertilization rate had to be expressed as a function of the total number of flowers per head to be comparable. Does this transformation mask a relationship between number of flowers per head (i.e. size of head) and number of flowers fertilized? There is a positive correlation between the number of flowers per head and number fertilized ($rho=0.1684$, $p<0.0001$), i.e. with more flowers per head more will be successfully fertilized. Are larger heads fertilized proportionally more than smaller heads? Are larger heads actively selected over smaller heads by pollinators? This is shown by dividing the number of flowers fertilized by the number of flowers per head, and then correlating this fertilization rate with the number of flowers per head. The relationship is marginally significant ($rho=-0.0561$, $p=0.0350$), indicating there is no

strong disadvantage to a larger head size.

The mean number of flowers per head differs significanly as a function of the number of flowering ramets per clone (Kruskal-Wallis test, $x^2=910.67$, df=12, $p<0.0001$), but no trend is discernible (Fig. 11). No significant correlation between number of flowers per head and the number of flowering ramets per clone exists (rho=0.0356, p=0.1813). This may reflect genotypic differences between the clones or variation in resource depletion within clones. As the distance between ramets increases (i.e. density within the clone decreases), so does the number of flowers per head (rho=0.3003, $p<0.0001$). Unfortunately the total number of heads per ramet was unknown, so no explanation of this phenomenon can be given. In general the ranges in the number of flowers per head for the clones overlap (Table 7). Of the eleven clones whose number of flowering ramets was greater than 3, eight had significant ramet to ramet differences in the number of flowers per head. Within a clone the ranges for individual ramets overlap completely.

If number of flowers per head is entered in the model, part of its effect is partitioned from the error term reflecting the variation in number per head within a ramet. The rest of its effect is partitioned from "clone" but most of it is returned to "position(clone)". This unexplainable behaviour caused me to exclude it from the model.

Figure 11.

The effect of clone size on floral head size. The mean number of flowers (ray and disc) per head as a function of the number of flowering ramets per clone. Bars indicate ±1 SEM.

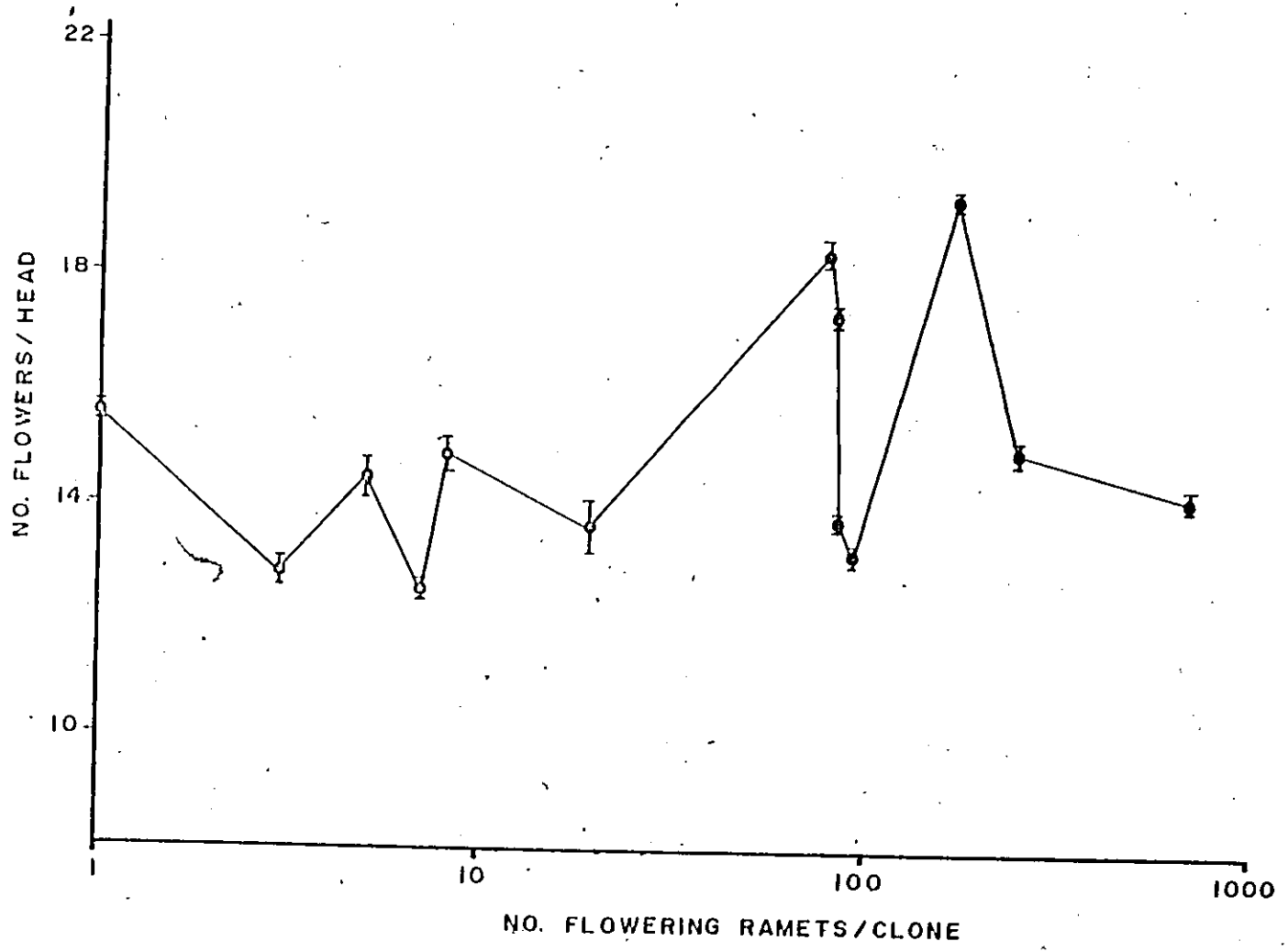

22
18
14
10
NO. FLOWERS / HEAD
1
10
100
1000
NO. FLOWERING RAMETS / CLONE

Table 7. Ranges of the number of flowers/head by clone.

CLONE	# FLOWERING RAMETS PER CLONE	RANGE	N(# HEADS)	MEAN ± SD
2	3	10-15	25	12.8 ± 1.15
4	1	15-20	15	16.5 ± 1.40
10	8	9-19	71	14.8 ± 2.28
11	7	10-15	45	12.5 ± 1.08
12	19	11-16	15	13.6 ± 1.64
13	5	10-17	35	14.4 ± 1.67
19	684	8-19	280	14.2 ± 1.64
20	84	9-18	122	13.7 ± 1.54
21	167	10-24	365	19.3 ± 2.09
30	82	14-20	110	17.2 ± 1.30
31	78	13-24	85	18.4 ± 2.00
32	91	9-17	96	13.1 ± 1.43
33	247	11-19	65	14.9 ± 1.60
60	1	16-21	15	18.5 ± 2.07
61	1	12-17	15	14.2 ± 1.26
62	1	13-17	15	15.4 ± 1.17
63	1	11-16	15	13.9 ± 1.40
64	1	9-18	15	15.1 ± 2.23
65	1	13-18	15	15.3 ± 1.45

3.2 Seed Predation

The larvae of Coleophora utilize different food sources as they age. Younger instars feed on reproductive parts before fertilization (floral or non-viable predation) and older instars feed on viable seed once the fertilization process is complete. Therefore, to examine predation in light of Root's (1973) resource concentration hypothesis the initial phase of predation (i.e. floral or non-viable) must be considered. This phase will more accurately reflect the female's response to patch size (i.e.number of flowering ramets per clone) when selecting potential oviposition sites. The inclusion of predation upon viable seed might distort the role of patch size selection, since interim processes (fertilization and resultant seed-set) determine the larva's subsequent food source. The magnitude of viable seed predation in each head will be the final determinant of a clone's total seed output.

The estimate of floral predation was obtained from pickled inflorescences sampled from each clone during the the flowering period. The flowers were beginning to set seed. The larvae were switching to these seeds, so this phase of Coleophora predation was essentially terminated. The mean percent floral predation per head was 6.27 ± 0.784. On the other hand, the estimate of non-viable seed predation per head was obtained from ramets harvested

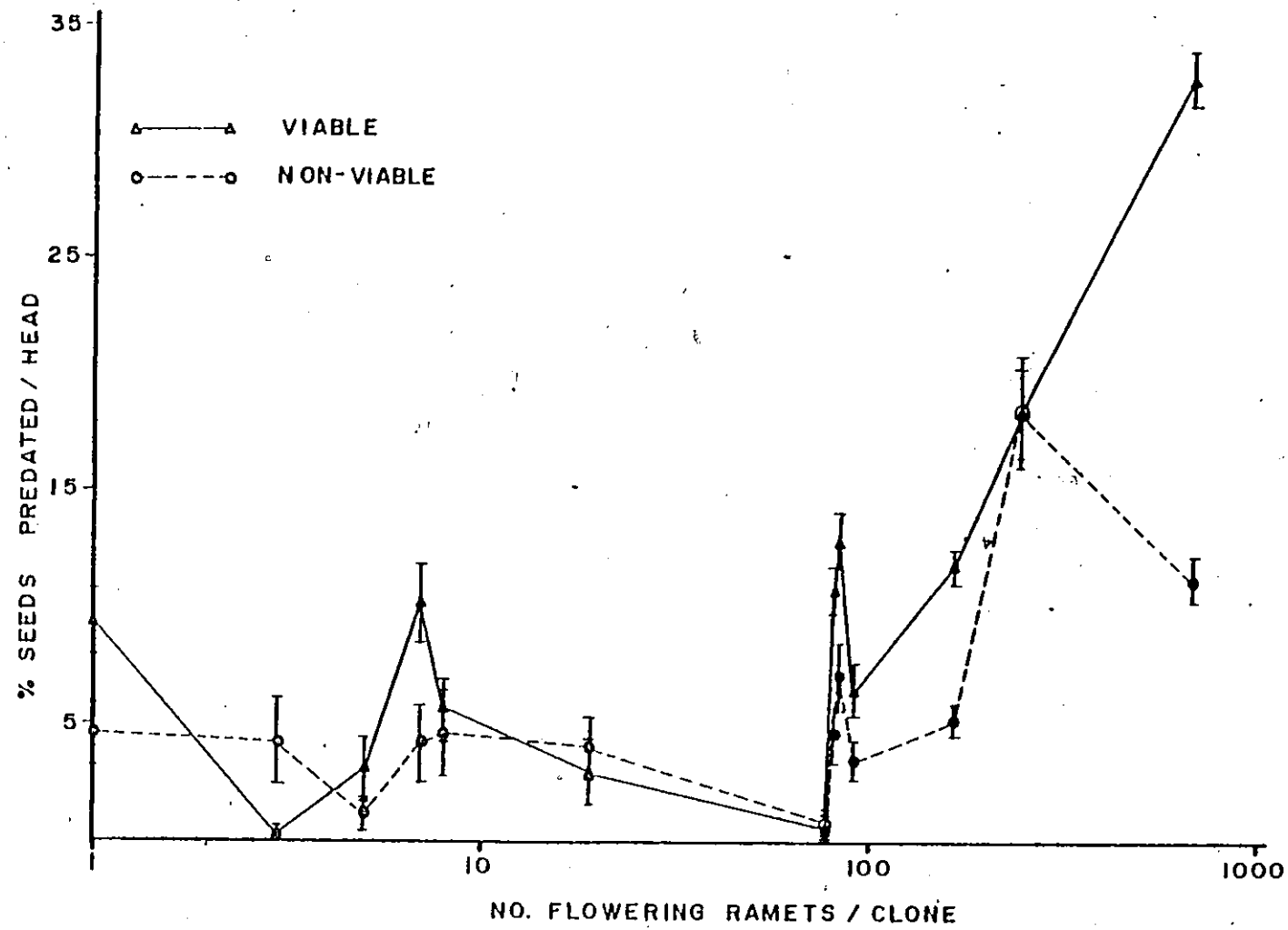
immediately before seed dispersal. The non-viable predated seeds were flowers that were never fertilized because the Coleophora larvae had consumed their ovules. The mean percentage of non-viable seed predation is 6.65± 0.359, the median is zero, and values range from 0 to 100%. At this stage most heads (66.69%) sustain no predation. These two predation indices are therefore thought to be analogous measures of the same predation pressure, i.e. damage inflicted by the early instar larvae of Coleophora sp.

In the flower results (Section 2.1) the amount of floral predation could not be discriminated on the basis of size of resource patch, measured by the number of flowering ramets. This, in part was due to the small sample size per clone. With the expanded sample size of the seed data set (n=1414 heads), significant differences in the mean percentage non-viable seeds predated per head can be detected as a function of the number of flowering ramets per clone (Kruskal-Wallis test, x^2=140.91, df=12, p<0.0001). The increasing trend (rho=0.2884, p<0.0001) is shown in Figure 12. It appears the female Coleophora can disciminate between patch sizes. Unfortunately details of the natural history of this lepidopteran are unknown. Are more ovipositing females attracted to larger patches, and/or are more eggs laid in larger patches by each female? Either would cause a greater intensity of predation per head.

Once the fertilization process is complete and the

Figure 12

The effect of clone size on seed predation. Comparison of the mean percentage of non-viable and viable seeds predated per head as a function of the number of flowering ramets per clone. Bars indicate ±1 SEM.


35
25
15
5
VIABLE
NON-VIABLE
% SEEDS PREDATED / HEAD
10
100
1000
NO. FLOWERING RAMETS / CLONE

seeds are maturing, the larva begins to consume viable seed. The mean percentage of viable seeds predated per head is $14.19 \pm 0.4598\%$, the median is 7.143% and entries range from zero to 78.57%. Only 44.48% of heads remain unpredated (0% predation). An additional 20% of heads are thus predated between the earlier fertilization period and the time of seed maturation. This suggests that, barring any new recruitment, each larva utilizes more than one head.

Compared to the larger clones, the single flowering ramet clones (n=7) are very heterogeneous in their predation intensities. (Note: these are not the same single ramet clones considered in the flower results). The percentage of non-viable seeds predated per head ranged from 0 (1 clone) to 12.73%; while the percentage of viable seeds predated per head ranged from 0 (3 clones) to 27.94%. The coefficient of variation for clones having only a single flowering ramet is 287.35 for non-viable seeds and 143.68 for viable seeds predation per head. By comparison, the coefficient is 201.69 for non-viable seeds, and 120.22 for viable seeds predated per head, for all other clone sizes combined.

The mean percentage of viable seed predated per head shows much stronger patch size differentiation than the early stage of predation. The means differ significantly as a function of the number of flowering ramets per clone (Kruskal-Wallis test, $x^2 = 406.71$, df=12, $p < 0.0001$) and the

increasing trend is much stronger (rho=0.4659, p<0.0001) (Fig.12). Why is there an exaggeration of patch size effect in the older instars? This could reflect an actual increase in the number of larvae per ramet in larger clones, which would force individuals to consume a greater proportion of a head, and/or it could reflect a high mortality rate in the smaller patches.

To assess the variation within clones between individual ramets, a Kruskal-Wallis test was performed on each clone (number of flowering ramets/clone > 1). Are the large within-clone differences ("position(clone)") seen in the fertilization rate (section 3.1) also encountered in the percentage predation per head? Only two clones of the twelve tested show any significant ramet to ramet differences in the percentage of non-viable seeds predated per head (Table 8). This conforms with the lack of positional effect found in floral predation (flower results). Since fertilization and non-viable seed predation occur simultaneously, the ramet to ramet differences seen in the fertilization rate would not necessarily be expected in this early predation. The early instar larvae do not depend on seeds for food. This is expressed in the lower correlation of non-viable seed predation to fertilization rate (rho=0.1428, p<0.0001). Since older instars feed strictly on seeds, the positional variation in fertilization rate within clones should be mirrored by the viable seed predation per head. Eight

Table 8. Ramet to ramet differences within a clone in seed predation using Kruskal-Wallis tests.

# FLOWERING RAMETS PER CLONE	DF	% NON-VIABLE PREDATED/HEAD x^2	% NON-VIABLE PREDATED/HEAD $p > x^2$	% VIABLE PREDATED/HEAD x^2	% VIABLE PREDATED/HEAD $p > x^2$
3	2	0.42	0.8112	0.08	0.9623
5	3	4.50	0.2123	12.50	0.0059
7	4	1.15	0.8857	5.19	0.2686
8	6	3.04	0.8033	3.99	0.6778
19	2	2.44	0.2945	6.00	0.0498
78	9	1.77	0.9947	1.39	0.9979
82	8	9.73	0.2844	37.04	0.0001
84	9	24.00	0.0043	38.83	0.0001
91	8	6.69	0.5405	22.12	0.0066
167	25	25.16	0.4535	114.87	0.0001
247	8	8.87	0.1811	25.59	0.0003
684	23	48.17	0.0016	80.97	0.0001

clones (Table 8) show significant ramet to ramet differences. The percentage of viable seed predated per head also has a much higher correlation with percentage of flowers fertilized per head (rho=0.5896, $p<0.0001$) than non-viable seed predation.

In plants with clonal growth, the concept of density is difficult to interpret. Density dependent predation may function at two (or more) levels: 1) overall density of S. canadensis clones in a neighbourhood would be an index of a clone's relative isolation from the nearest conspecific and 2) density within that individual clone could influence, in conjunction with patch size, its "attractiveness", with respect to the perception of the Coleophora moth.

Is there any protection afforded by isolation and interspersion within the diverse background of this complex community? An aggregation of clones could further concentrate the resource and make detection easier. The more clones in a five metre area, the higher the percentage predated, both of flowers and viable seeds (non-viable predation/head rho=0.2053, $p<0.0001$; viable predation/head rho=0.2220, $p<0.0001$). (Note: viable predation/head is probably marginally higher because of fewer zero values. See section 3.13 for reasons for such a slight correlation.)

Density within clones may also influence intensity of predation. As distance to the next flowering ramet increases (i.e. density decreases) there is a slight

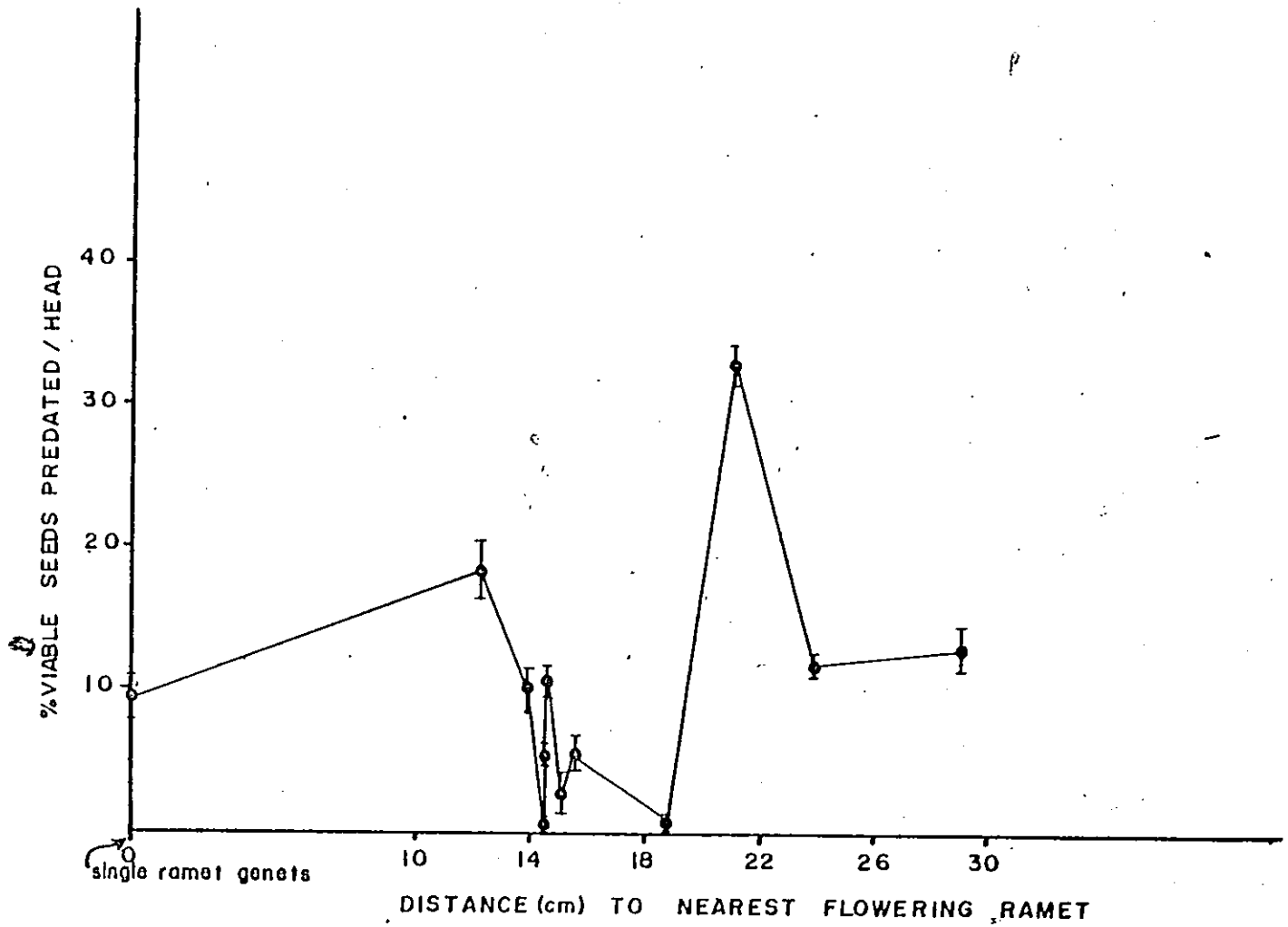
increase in predation intensity (non-viable predation/head rho=0.0562, p=0.0347; viable predation/head rho=0.1366, p<0.0001), but the trend is weak enough to ignore for either phase (Fig.13). This correlation may be the result of the correlation of percentage of flowers fertilized per head with distance to the nearest flowering ramet within a clone (section 3.14). There is also a relationship between number of flowering ramets per clone (a measure of clone size) and distance to the nearest flowering ramet (rho=0.452, p<0.0001). Since predation intensity is positively correlated to the number of flowering ramets, the increase with decreasing density may simply reflect this cross-correlation. Unfortunately, the contribution of these variables cannot be evaluated in a single model as they were in the analysis of seed-set because of difficulties in meeting the assumptions of Analysis of Variance.

3.3 Seed Output

Only when the larvae cease feeding and cap their silken cocoons, can the final seed output be evaluated. These are the viable seeds that may ultimately propagate that genotype. The mean percentage of viable seeds per head differs significantly as a function of the number of flowering ramets per clone (Kruskal-Wallis test, x^2=125.62, df=12, p<.0001). This mirrors the clones' contrasting

Figure 13

The effect of clonal inter-ramet density on seed predation. The mean percentage of viable seeds predated per head as a function of distance (cm) to the nearest flowering ramet within a clone. The genets with only one flowering ramet are represented at zero cm. Bars indicate ±1 SEM.


% VIABLE SEEDS PREDATED / HEAD
40
30
20
10
0
single ramet genets
10
14
18
22
26
30
DISTANCE (cm) TO NEAREST FLOWERING RAMET

predation intensities. The percentage of viable seeds predated per head has a stronger trend with number of flowering ramets per clone (rho=0.4689, $p<0.0001$)(Fig.12), than the percentage of flowers fertilized per head (rho=0.3483, $p<0.0001$)(Fig.8). Larger clones suffer proportionally more predation per head. As a result the proportion of seeds escaping intact, has a slight negative correlation (rho=-0.1539, $p<0.0001$)(Fig.14) with the number of flowering ramets per clone.

Figure 14 depicts an interesting relationship between the percentage of viable seeds predated per head and the resultant percentage of viable seeds per head with clone size. Smaller clones have a proportionally higher percentage of the ovules fertilized in a head escaping predation as viable seeds (i.e. the curve relating percentage viable seeds per head to clone size is above that for percentage of viable seeds predated per head). This relationship reverses for very large clones, with the transition occuring between 82-167 flowering ramets per clone. These trends can be more easily identified by expressing each function as a percent of the total percentage of flowers fertilized per head for each clone size as shown in Table 9. In smaller clones (number flowering ramets < 78) the percentage of viable seeds per head is larger than the percentage of viable seeds predated. Again, more seeds of the total fertilized, escape predation. In intermediate-sized clones (82-167

Figure 14

The effect of clone size on resultant seed produced per head after seed predation. The mean percentage of flowers fertilized per head, the mean percentage of those viable seeds predated per head and the resultant mean percentage of viable seeds per head the escaped intact as a function of the number of flowering ramets per clone. Bars indicate ±1 SEM.

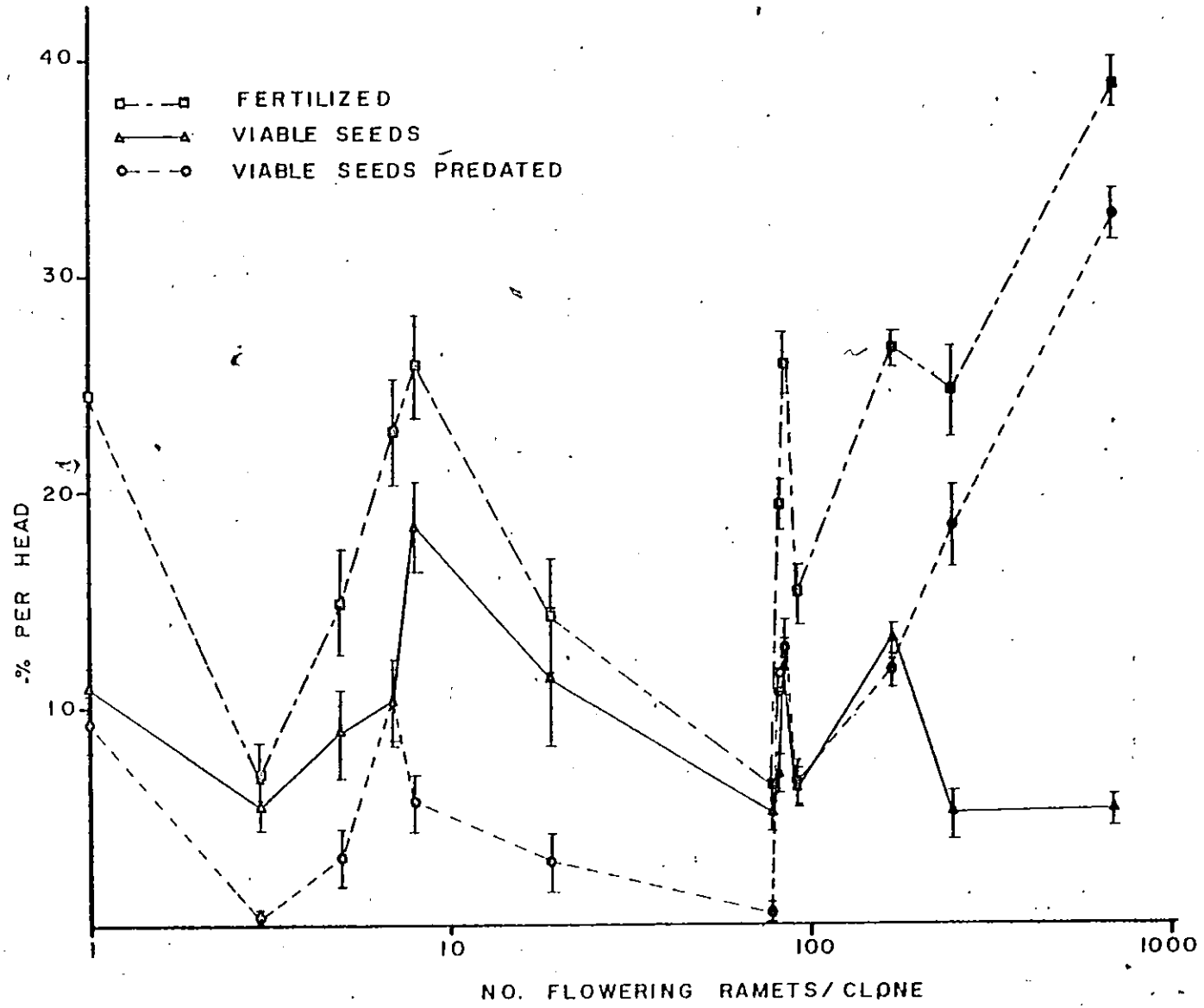

FERTILIZED
VIABLE SEEDS
VIABLE SEEDS PREDATED
40
30
20
10
% PER HEAD
1
10
100
1000
NO. FLOWERING RAMETS/ CLONE

Table 9. Percentage viable seed predation and viable seed produced expressed as a percent of the total percentage fertilized/head.

# FLOWERING RAMETS PER CLONE	$\frac{\text{MEAN \%VIABLE PREDATED/HEAD}}{\text{MEAN \%FERTILIZED/HEAD}}$ X 100	$\frac{\text{MEAN \%VIABLE/HEAD}}{\text{MEAN \%FERTILIZED/HEAD}}$ X 100
1	37.98	44.10
3	3.94	80.43
5	20.52	60.40
7	44.64	44.80
8	21.50	71.27
19	20.09	79.92
78	10.76	78.90
82	54.94	35.77
84	49.49	46.12
91	42.39	41.86
167	44.40	49.65
247	74.74	20.69
684	84.40	13.67

flowering ramets per clone) the two account for an equivalent proportion of the total potential seeds. In the largest clone (247,684 flowering ramets per clone) the percentage of viable seeds predated is much greater.

Why does this size threshold exist? What determines how successful the larvae are in depressing seed output? The average dry weight of a mature (capped) larva is 0.737± 0.0758 mg (n=10). The average viable seed weighs 0.092± 0.0005 mg (Table 10), of which 0.015 mg is pappus , leaving 0.077 mg consumable biomass per seed. If the assimilation efficiency of a larva is assumed to be 40% (Price 1975), then 23.9 seeds (0.737/(0.077x0.4)) are needed to support one larva over the seed-eating period. Hawthorn and Hayne (1978) found the larva of a closely related microlepidopteran, Metzneria lappella (Gelechiidae) consumed from 2 to 15 seeds of burdock, with means of 7 to 9 per individual. Seeds of burdock are much larger than those of goldenrod, so that the calculated consumption per Coleophora larvae is at least reasonable. This figure is most likely an under-estimate, since the formula only considers the final larval weight, ignoring maintenance energy. Also the change of food type (ovules to seeds) with age, and any possible change of efficiency in the different instars (Waldbauer 1968), are not considered.

Therefore, the number of heads a larva must visit will depend on the number of flowers fertilized per head and their dispersion within the ramet. In clones with higher

Table 10. Mean seed weights.

SEED CLASS	N	MEAN ± SD (mg)	RANGE
Non-viable	3384	0.022 ± 0.0069	0.007-0.048
Partially filled	756	0.043 ± 0.0148	0.012-0.102
Viable	2167	0.092 ± 0.0211	0.035-0.208

fertilization rates per head, fewer heads need be attacked. The variability in food resource (percentage of flowers fertilized/head) can be evaluated using the coefficient of variation. This coefficient allows one to compare the amount of variation in populations (clones) having different means (Sokal and Rohlf 1969). If the number of viable seeds per head is variable (a higher CV), a larva would be forced to visit a greater number of heads, and to move between heads more often. This increased movement increases exposure of the larva to predation. Table 11 shows the Coefficient of Variation of the percentage of flowers fertilized per head for each clone. The smaller clones generally have higher coefficients than larger clones, indicating the more variable nature of the resource. This is also reflected in the coefficients of the percentage of viable seeds predated per head (Table 11). Variability of the primary food source translates into a higher variability in the probability of a head being attacked. If this variability in food source in smaller clone results in higher larval mortality rates, these clones would suffer proportionally less predation than larger clones. More seeds would be left intact. This would also explain the exaggeration in the patch size effect in percent viable predated per head (section 3.2). A more reliable food source reduces mortality rate, more larvae survive, so larger clones suffer greater damage.

The single flowering ramet catagory (Table 11)

Table 11. Means and coefficients of variation for the percentage fertilized/head and the percentage viable seeds predated/head classed by clone size.

# FLOWERING RAMETS PER CLONE	MEAN %FERTILIZED/HEAD	CV	MEAN %VIABLE PREDATED/HEAD	CV
1	24.48	59.72	9.30	143.68
3	6.78	119.33	0.27	500.00
5	14.72	89.97	3.02	276.92
7	22.68	72.73	10.13	109.37
8	25.77	76.34	5.54	191.46
19	14.17	75.33	2.84	178.83
78	6.40	114.66	0.69	419.07
82	19.44	61.66	10.68	108.25
84	25.93	63.05	12.83	120.99
91	15.31	87.79	6.49	161.80
167	26.58	61.71	11.80	114.78
247	24.67	70.93	18.45	84.09
684	38.91	47.37	32.84	60.05

combines seven different clones (genotypes). Considered together, the mean percentage of flowers fertilized per head is high (24.48%) and hence the CV is low (Table 11). However, the CV for percentage of viable seeds predated per head is comparatively high. Being different clones, the intensity of predation between clones varies greatly, and does not always reflect the amount of resource available (i.e. percentage of flowers fertilized per head (Table 12). Relatively low infestation rates result in high CV's while other ramets sustain no damage. The resource may not be as variable, but the probability of finding single flowering ramets may be smaller.

The determinants of final seed output are all viewed with respect to the basic floral unit of S. canadensis, the head. Each aspect has been considered as a function of clonal growth. The question is: what are the repercussions of clonal expansion, and the concomitant increase in the number of flowering ramets? It has been established that there is an increase, not a decrease, in percentage of flowers fertilized per head as the clone expands, but there is a synchronous, larger increase in the percentage of seeds predated per head. The final outcome is that a smaller proportion of seeds per head escape intact from these larger clones. These processes must also be viewed with respect to the clone as a unit. It is obvious that given the increase in the number of total flowering ramets as the clone grows, larger clones still maintain a much higher net output of viable seed.

Table 12. Means and coefficients of variation for the percentage fertilized/head and the percentage viable seeds predated/head for single flowering ramet genets.

CLONE	MEAN %FERTILIZED/HEAD	CV	MEAN %VIABLE PREDATED/HEAD	CV
4	19.59	77.25	1.69	296.30
60	27.72	47.29	0.00	0.00
61	28.55	51.72	20.04	59.10
62	25.41	63.56	0.00	0.00
63	23.08	56.90	0.00	0.00
64	17.99	81.43	12.31	87.67
65	29.34	49.46	27.94	46.04

DISCUSSION

1. Patterns of Flowers Fertilized per Head.

The analysis of fertilization rate allowed me to partition out each variable's effect from its relevant level of nest within the model. This section of the discussion will consider 1) differences between clones in terms of input variables, and factors that could possibly contribute to the small amount of unexplained variance; 2) differences between ramets within a clone, in terms of variables operating at this level and potential reasons for the very large amount of unexplained variance; and lastly 3) possible factors elucidating the large residual term, head to head variation.

1.1 Differences Encountered Between Clones.

1.11 Number of flowering ramets per clone and the intra-clonal ramet density.

The fertilization of flowers in Solidago canadensis is an interactive process involving many input variables. In this model the most important variable considered is floral patch size or number of flowering ramets per clone. An increase in patch size, especially in an incompatible plant species, may have somewhat an anomalous effect (Carpenter 1976, Heinrich 1975). This problem has prompted numerous studies whose subjects range from agricultural plants such

as orchard fruit trees (Free 1960,1966) to more natural aggregations such as tropical trees and shrubs (Augspurger 1980, Frankie et al 1976).

The massive flowering display of a clone provides a large potential resource, when coupled with the energetic demands of the flower visitors, will delineate flower to flower and clone to clone movement (Heinrich 1975). Since such a large aggregation of available resource provides a greater nectar and/or pollen reward per unit area than a more dispersed food source, travel between clones should be restricted. By clustering flowers into heads, many heads into a ramet, and having relatively closely spaced ramets within a clone, many intra- and inter-ramet visits would be expected in S. canadensis. As a result of this expected conservative pollinator foraging behaviour, lower seed-set with increasing floral patch size is predicted. The hypothesis is clearly not borne out in this study. There was no apparent suppression of seed-set per head with increasing patch size. The increase in the number of ovules fertilized per head must be mediated by an increase in the number of effective pollinator visits, since autogamy is not an alternative breeding system. The size of the potential resource is thus important in attracting pollinators, whether it is a plant with only one flowering stem, a clone, or a tree. Intra-clonal density (i.e. distance to the nearest flowering ramet) is also an important cueing factor in initially attracting

pollinators. In S. canadensis, as well as other clonal species, it is difficult to separate the effects of size and density on the foraging behaviour of the pollinators.

Each ramet in larger clones attracted a greater number of visitors, and more importantly, greater numbers of the pollinator, Chauliognathus. Greater numbers of pollinators result in increased seed-set per head with greater clone size. The actual foraging dynamics of Chauliognathus within a clone and the resulting pattern of fertilization, will be discussed in more detail later in this section. Size or density dependent foraging by pollinators is prevalent in many other plant species. On Cayler Prairie, larger clumps of Astragalus canadensis L., the milk vetch, received more bumblebee visits than smaller clumps (Platt, Hill and Clark 1974). Experimentally generated populations of Liatris pycnostachya Michx., established at differing densities, attracted more pollinators (Bombus pennsylvanicus) at high than low densities (Schaal 1978). In the tropics, density dependent foraging has been shown in shrubs and trees (Augspurger 1980, Johnson and Hubbell 1975, Silander 1978). Larger inflorescences (umbels) of the common milkweed, Asclepias syriaca L., had higher insect visitation frequencies than smaller inflorescences, but also had more nectar thieves, which did not achieve pollination and fertilization (Willson and Price 1977, Willson and Bertin 1979). This increase in non-pollinating visitors is apparent in S. canadensis (Fig. 3). No attempt

was made to quantify the effect of increasing nectar and/or pollen thievery on seed-set, since each act removes such minute quantities that it was impractical to assess.

Although floral patch size is the most important variable considered in this analysis, it accounts for a relatively small proportion of overall seed-set variation. The outcome of this study indicates the percentage seed-set per head is not a consequence of the mass-flowering phenological pattern alone. Many biological variables influence ovule fertilization, both at the clonal level and within individual clones. The rest of the model considers these.

1.12 Distance to the nearest S. canadensis clone.

Since successful fertilization depends on the availability of other clones for cross-pollen, spatial aggregation of individual clones must be considered. Silander (1978) and Augspurger (1980) also found a negative relationship between seed-set and nearest neighbour conspecific distance. Energetic demands of the pollinator, as well as spatial distribution of genotypes (clones), influences the rate of inter-plant movement. This rate defines the amount of cross-pollen available for fertilization. Chauliognathus utilizes multiple species concurrently. Perhaps aggregated clones influence the probability of the beetle flying to a conspecific, rather than flying to another species and wasting pollen. The

frequency of inter-clone or inter-specific movement by Chauliognathus was not monitored and therefore cannot be linked with the response of seed-set to clonal dispersion on Cayler Prairie.

Inter-plant movement of pollinators has been monitored in several mass-flowering tropical plants. In a study of Andira inermis (Swartz)HBK (Frankie et al. 1976), a large, self-incompatible tree, inter-tree movements by solitary bees occured at a very low rate. Only 0.3 to 3.8% of marked bees were recaptured on another tree. Also, more bees were recaptured from trees closest to the trees from which they were released than from more distant trees. This low inter-genotype pollen transfer caused very low fruit set (0.4 to 1.8% reported in Augspurger 1980). Frankie et al. (1976) suggested that this low rate of inter-plant movement was due to the spatial pattern of the particular population studied in which trees were widely spaced. In Hybanthus prunifolius (Violaceae), a self-compatible shrub that requires bee pollination for successful fertilization, Augspurger (1980) suggests that high out-crossing can be realized because of high spatial density, resulting in high inter-plant movement.

Since individual clones are rather large resource pools, it is questionable if the pollinator's visual capacity can evaluate aggregations of clones. A size threshold may exist. This may also contribute to the rather low correlation of overall clone density and

seed-set.

1.13 Percentage of stigmas clipped per head.

In these studies the stigma clipping per head in different clones ranged from 25 to 72% with a mean of 45%. Floral predation in Lupinus amplus by the larvae of a lycaenid butterfly reached well over 50% in certain areas of Colorado (Breedlove and Ehrlich 1968). Such intense levels of floral predation are rarely reported. The lack of a patch size dependency in the amount of clipping reflects the gregarious nature of Epicauta (Horsfall 1943), the availability of alternate food sources (Root 1973) and the large populations observed on Cayler Prairie. Differences in amount of stigma clipping per clone are manifested but not in conjunction with clone size. Since pollination and clipping occur concurrently, actual pollinator effectiveness is masked. In the model the extent of clipping damage per head is the second most important determinant of seed-set. It sets the upper limit for potential pollination. Stigma clipping by Epicauta complicates interpretation of how the fertilization process responds to individual and population density. Nothing further can be said about the biological importance of stigma clipping as a clonal descriptor, since detailed information is lacking.

1.14 Floral predation per head.

The last covariate of importance in understanding differences between clones is floral predation by the early instar larvae of Coleophora. Direct links to fertilization rate are difficult to extract because of the negative correlation of floral predation with clipping rate. It is the least important determinant of seed-set in the model, accounting for only a small amount of the variance between clones. Any further comment on its role in the fertilization process would be ill-advised without more intensive investigation.

Floral predation is also found in Helianthus annuus (Compositae). Rogers (1978) reported that larvae of the sunflower moth interfere with the fertlization of the annual sunflower by chewing through the corolla and severing the stigma before fertilization can occur. Floral destruction (both stigma and ovary) by one larva resulted in 133 empty achenes among over 200 possible from a head. Commercial sunflowers are self-compatible. Therefore damage depends upon the number of ovaries self-fertilized before severance of the style. In Solidago the damage is more pronounced. Once the ovary or floral parts are attacked, a flower can no longer form a seed. To the best of my knowledge no other studies have considered the effects of concurrent predation and pollination of flowers on actual seed-set. Beattie, Breedlove and Ehrlich (1973) show that the monument plant, Frasera, sustains very low

floral predation (5%), but they do not link it with how seed-set is affected. Janzen (1971b) suggests flower eating may lower seed output but maintains that flower crop size is only loosely correlated with seed crop size. No reference is made to the potential interference with the pollination process.

The role these two sources of floral predation, stigma clipping and ovule destruction, play in shaping an "optimal" infloresence size (i.e. number of flowers per head) will be discussed in a later section.

1.15 Unexplained variance: Potential Sources.

The final amount of fertilization is the culmination of a "heirarchy" of effects. Each effect in itself responds differently to clonal parameters. The model used to account for observed fertilization patterns considered only a few of the possibilities. One of the other possible factors is unequal herbivore pressure between clones.

Early in the growing season Solidago is attacked by the larvae of three species of goldenrod beetle, Trirhabda. They graze on leaves and often consume most or all of the young foliage (Werner et al. 1980). Pupation occurs early in July and the adults emerge a few weeks later. Adults also feed on goldenrod leaves. Werner et al. (1980) state that in most years infestation levels are rather low, but outbreaks have been recorded. Where entire populations are devastated new basal stems are produced in September, but

sexual reproduction is lost for that year.

In 1979 Trirhabda spp. were below outbreak proportions on Cayler Prairie. Since the entire goldenrod population was not erradicated, differential grazing between clones is a possiblity. Energy for infloresence growth in S. canadensis is supplied exclusively by the upper leaves in each ramet (Bradbury and Hofstra 1977). Grazing concentrated in these leaves would reduce energy available for infloresence growth. As a result both inflorescence size (number of heads per ramet) and total ramet height would be depressed. I did not collect data to document grazing effects between or within clones. There are also possibly genotypic differences between clones in total height and inflorescence size. Regardless of cause, height and inflorescence size do vary between clones (pers. obs.). These differences in physical parameters may influence the number of pollinator visits and their fidelity to that clone, especially if the pollinators exhibit horizontal flight behaviour (i.e. pollinators tend to remain at a certain height above ground when flying between plants and will bypass flowers above or below this height) (Waddington 1979).

Differences between clones in the mirid (Miridae: Hemiptera) faunal load (Messina 1978), and hence amount of phytophagous insect damage would also contribute to unaccounted variance between clones. No data were collected to document any possible differences.

In summary differences encountered between clones in seed-set are the product of many, often unaccounted sources of variation. The hierarchy of seed-set determinants begins with herbivory, is followed by ovule predation and stigma clipping, each of which is responsive to different factors, and finally ends with the actual pollination and fertilization processes After monitoring the outcome, seed-set per head, the plethora of input factors is difficult to assess in retrospect.

1.2 Differences Encountered Between Ramets Within a Clone

1.21 Percentage of stigmas clipped per head and floral predation per head.

The fertilization dynamics within the clone, i.e. ramet to ramet differences in seed-set, will now be considered. In the model, only the clipping damage and ovule predation per head varied both between clones and between ramets within a clone. The total effect of these two variables could not be evaluated because individual ramets were assigned location means as estimates in the model. This constrained the total variation and true differences between ramets were masked. If both stigmas clipped per head and floral predation per head had been evaluated for each ramet, more variation would have been extracted from the 'position(clone)' term. The variation in seed-set accounted for by these two predation sources was therefore underestimated in the model.

The two covariates considered accounted for very little of the total variation in seed-set at the ramet level of nesting. As a result a large proportion of the between ramet differences remains unexplained. The reasons behind these large ramet to ramet differences in seed-set must be explored in more detail, especially since it is the pollinator foraging behaviour at this level that determines the actual relationship of seed-set to clone size. The target is the ramet, not the clone.

1.22 Unexplained variance: Potential Sources.

It is conceivable that herbivore pressure may differ between ramets within a clone, resulting in height and inflorescence size differences. These morphological parameters do differ within a clone, as they did between clones. Limited energy available for inflorescence growth may account for the observed differences in the mean number of flowers per head between ramets within a clone. Additional variance would have been removed from the term 'position(clone)', had these parameters been included in the model.

Cayler Prairie is an unique area when considering the pollinators of S. canadensis. Goldenrod's regular pollinators, which include bumblebees and honeybees, do not visit the plant. In this area, possibly due to its relative isolation from other natural (i.e. not farmed) reserves, there is an overall paucity of pollinators (Platt

et al. 1974, R. Cruden, pers. comm., and pers. obs.). Competition among plants for the most efficient pollinators (Levin and Anderson 1970, Waser 1978b) should therefore occur. If pollinators are indeed a limiting resource then seed-set should vary as a function of their activity (Zimmerman 1980a). High energy pollinators such as bumblebees, honeybees, wasps, and syrphid flies expend more energy than low energy pollinators due to high metabolic costs of flight and thermoregulation. As a result they will forage on the most energetically rewarding flowers (Heinrich 1975). It is for this reason that S. canadensis attracts mainly low energy pollinators such as beetles on Cayler Prairie. Usually bumblebees will continue to sample the less rewarding species such as Solidago to "track" temporal changes in the resource spectrum (Heinrich 1976,1979a). Since no bumblebees (or other bees) were ever observed on S. canadensis, the contention that the number of available pollinators is extremely low is reinforced. Bees did visit other, larger-flowered Solidago species (e.g. S. rigida and S. missouriensis).

I believe it is the restricted gut capacity of the major pollinator, Chauliognathus, that in part explains the remaining large ramet to ramet differences in seed-set. Suppose a beetle becomes satiated after visiting only one ramet and departs, without visiting another ramet within that clone. Then seed-set will be a function of the number of visits a ramet receives during its entire flowering

time. The number of pollinator visits is dependent on floral patch size. Larger clones receive more visits per ramet. Three lines of evidence support this explanation: 1) The beetle's behaviour fits this hypothesis. The beetle flies onto the base of an inflorescence, walks up the stem to the bottom branch and begins to forage on nectar and pollen, working each branch in quick successsion. The beetle may stop and rest, or bask in the sun and then continue feeding. Harvesting the resource is inexpensive since flight is not required. All branches on a ramet are visited, moving from the bottom to the top of the inflorescence, but not all heads are probed. After feeding is complete, the beetle walks to the end of the branch, preens itself and flies off, but not necessarily onto a neighbouring ramet. This suggests that the beetle is satiated. If a beetle were not satiatied it should fly to the nearest food source, a neighbouring ramet. 2) Seed-set did not decrease over a very wide spectrum of resource patch sizes, instead it increased. This reinforces the idea of limited intra-clonal flights. Low rates of intra-clonal movement by the beetle would restrict the distribution of geitonogamous pollen, which would obviate the expected seed-set depression with increasing clone size. 3) Indirect evidence suggests that increased ramet density within a clone did not lead to increased numbers of inter-ramet flights by the pollinators, since seed-set did not decrease.

These observations suggest that the beetle treats each ramet as a single resource, which provides ample food for satiation. Foraging behaviour has been shown to vary with the levels of satiation in mantids (Charnov 1976). Unfortunately no evidence is available on the foraging energetics of beetles. Beetles are primitive, non-specialized pollinators. Others consider them to be poor fliers (e.g. Faegri and van der Piji 1971) but I have observed long flights many times on Cayler Prairie. Typical "beetle flowers" are large, dish or bowl shaped, with exposed anthers or small clustered flowers aggregated into flattened inflorescences (Meeuse 1959).

Social bees, on the other hand, are not easily satiated because they forage for the colony as a whole and not solely for themselves. Their foraging behaviour has been evaluated more accurately since many complicating behaviours, such as territorial defense, searching for mates, preening and eating pollen etc. that are usually seen in beetles, are absent (Heinrich 1979a). For these reasons the foraging behaviour of social bees, mainly bumblebees, has been used in models of "optimal foraging theory" (e.g. Pyke, Pulliam and Charnov 1977) and many "rules" of movement have been quantified. Examples of these "rules" are movement between flowers within inflorescences (Pyke 1979) and between inflorescences (Pyke 1978a). These programmed behaviours, together with plant properties, result in co-evolved pollination systems (Pyke

1978b, Heinrich 1979b). Bees (high energy pollinators) would visit many flowers per inflorescence and then move to the nearest neighbour, which in S. canadensis would be the adjacent ramet. Beetles (low energy pollinators) do not seem to be as energetically constrained as bees, and so do not move between ramets. The lack of bee visitors and replacement by beetles on Cayler Prairie may therefore result in totally different levels and patterns of seed-set than experienced in old fields.

In varying degrees bees also tend to be site and flower specific (i.e. constant to one or few species) (Heinrich 1976). Unfortunately such detailed studies are lacking for beetles. No measure of an individual soldier beetle's flower constancy was made, although beetles were seen on all other blooming composites. Waser (1978b) reported seed-set reduction in two mountain perennials during their brief overlap in flowering period. The reduction resulted from interspecific pollen transfer by their common pollinator, the Broadtailed Hummingbird. Any interspecific transfer of pollen by Chauliognathus may cause seed-set reductions due to wastage of pollen, pre-emption of the stigmatic surface and loss of effective pollinator visits.

The relative amounts of cross-pollination and hence seed-set accomplished by bee versus beetle pollinators would depend upon cross-pollen transferred as they visited subsequent heads and ramets. Levin and Kerster (1974) cite

several studies that indicate pollen carryover is minimal, i.e. most pollen is deposited on the first stigma and little pollen is carried past the third stigma. Hartling and Plowright (1978), working with bumblebees and red clover, and Thomson and Plowright (1980), working with several bumblebee-pollinated flowers (2 species of Liliaceae and one of Caprifoliaceae), have found pollen carryover to be much higher than previously expected. Pollen deposition declined in a "roughly" exponential fashion as a function of the number of flowers visited. The number of pollen grains deposited was highly variable. The flowers used in these studies were relatively large, discrete units with a more definable pollination system, i.e. the bees must fly to each flower individually. Since Solidago has "mess and soil" pollination, pollen carryover should be more complex. The actual dynamics of pollen deposition would be linked to the distribution of pollen on the insect's body.

Both bees (Heinrich and Raven 1972) and beetles visit many heads per ramet. The head architecture of Solidago may aid in the transfer of cross pollen, and hence pollination effectiveness. As the insect walks over the head, the ring of mature female ray flowers will trap cross-pollen before it is replaced by geitonogamous pollen being produced by the central male disc flowers. Primack and Silander (1975) contrasted the pollination effectiveness of Apis mellifera L. (honeybee) and

Chauliognathus marginatus Fab. in the evening primrose, Oenothera fruiticosa L. They monitored number of flowers used, level of outcrossing and efficiency of pollen transfer. Beetles stayed longer in each flower, visited fewer flowers and carried fewer pollen grains than bees. They calculated 71.2% of the bee's pollen was cross-pollen, while 63.5% of the beetle's load was cross-pollen. Indeed, soldier beetles can be efficient pollinators. The proportion of cross-pollen carried will vary with type, size and spatial pattern of flowers. Primrose flowers are large individual units and are not as easily harvested as the aggregated heads of S. canadensis. In the goldenrod, if a bee visits many heads per ramet and then visits other ramets within that clone, very little cross-pollen is likely to filter past the first ramet. So beetles may accomplish the same amount of cross-pollination as bees, even though they only visit one ramet. Also, by restricting movement to one ramet per clone the beetle would spread less geitonogamous pollen within the clone than a bee. In the same way interspecific pollen reduces fecundity, geitonogamous pollen complexes the relatively small stigmatic areas of S. canadensis and precludes subsequent cross fertilizations.

Plants relying on animals for pollination should present resources in a way that maximizes pollination but minimizes cost of nectar and/or pollen production (Heinrich 1975). The optimal temporal pattern and concentration of

nectar production depends on the class of pollinator considered and their energetic demands. Plants adapted for out-crossing should produce enough nectar to attract pollinators, but limit production to force them to visit other plants of that species (Heinrich and Raven 1972). Heinrich and Raven believe that composites are able to maintain out-crossing despite small caloric rewards per inflorescence, because of their aggregated heads, dense colonies and long flowering time. This enables high energy pollinators to forage profitably. As a species, Canada goldenrod clones are available to foragers for more than one month.

Individual S. canadensis clones bloom for about two weeks. Both pollen and nectar rewards are renewed as new disc flowers open in each ramet. Once the clone begins to flower it represents a constant, predictable source of food. The predictability of the resource, ease of extraction and low harvesting cost should guarentee repeated visits to the ramets by pollinators. This does not imply constancy or memory within the insects.

Long periods of floral presentation also benefit the plant. According to Burtt (1961), the "chief functional characteristic of a capitulum" (head) is the long time period over which a succession of stigmas is presented. This avails the stigmas, individually and as a unit, to many possible pollination events. Burtt (1961) also suggests that the heads' potential for mulitple pollination

visits produces seeds derived from several different pollen parents. The biological predisposition for multiple visits per head over time, constant replenishing of resources and the satiation of the soldier beetle enable this population of Solidago canadensis to achieve an adequate seed-set despite the absence of high energy, more efficient pollinators and the increase in floral patch size.

There is a potential incongruency in the previous argument. Why would pollinators respond to increased patch size if only a fragment (i.e. ramet) of the total resource is utilized? Limited use of a large resource has been observed in several studies. Schmidt (1980) found that butterflies (low energy pollinators) generally visited only one of many heads avialable in Senecio spp. (Compositae). Melipona interrupta, a social bee, visited only 5% of available flowers on the mass-flowering shrub, Hybanthus (Augspurger 1980). In Caesalpinia pulcherrima, a small tropical tree with many flowers aggregated into an inflorescence, Cruden and Hermann-Parker (1979) found that butterflies visited only 4 to 6 flowers per tree on any foraging trip.

Inter-plant movement may result from several other factors. Increased aggressive interactions as the number of visitors increase with increased patch size or nectar availability, may drive individuals to another plant. An increase in pollinators may attract more of their predators ("anti-pollinators"), causing pollinators to disperse from

the plant. Neither increased aggression nor the occurrence of anti-pollinators were evaluated as potential mechanisms inducing inter-plant movement.

In summary, large ramet to ramet differences in realized fertilization estimates may be partially explained by differences in the clipping and floral predation rates per head, herbivory, inflorescence size, potential satiation of Chauliognathus on one ramet and the number of pollinator visits per ramet.

1.3 Head to Head Differences Within a Ramet.

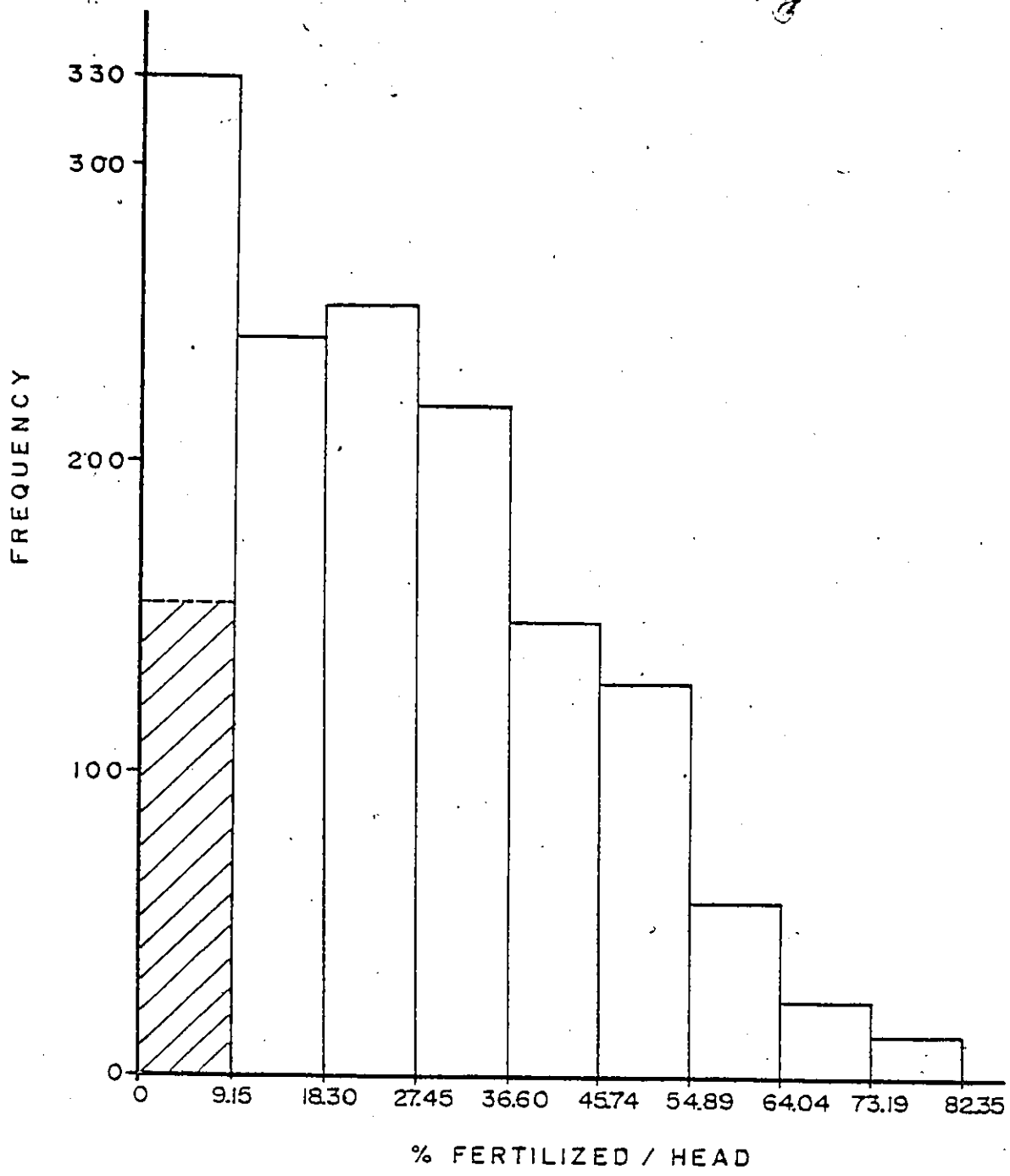
The largest unexplained variance in seed-set is found between heads within a ramet, the lowest level of the nest. Between head variation accounts for over 50% of the variation in percentage of flowers fertilized per head. Apart from any biological explanation, the "lack of fit" (Draper and Smith 1966) of the model would fall into this residual catagory. Its magnitude can not be separated from pure error by the statisical methods used.

Biologically, head to head response in fertilization is highly variable as a result of the decay rate of cross-pollen transferred as the beetle forages within a ramet. As mentioned, Thomson and Plowright (1980) suggested that the amount of cross-pollen manipulated by the insect declines in an exponential manner with the number of flowers visited. This pattern of pollen decay is reflected by the frequency distribution of percentage

fertilized per head (Fig. 15). As a beetle alights on an inflorescence and commences foraging, any receptive stigmas contacted by the beetle will receive out-cross pollen. This initial transfer of out-cross pollen results in a high proportion of flowers within these first heads being successfully fertilized. As the beetle continues to forage within a ramet, cross pollen is rapidly replaced by geitonogamous pollen. Replacement rate should be a function of the number of heads, specifically number of male disc flowers, contacted by the beetle. The exchange of pollen means that a smaller proportion of flowers per head will be successfully fertilized as the number of heads visited within an inflorescence increases. Residual out-cross pollen on the beetle's body will allow for progressively lower rates of fertilization. This pattern and rate of pollen deposition and uptake results in the observed variation in seed-set per head. There are very few heads with a high proportion of flowers fertilized; and a progressive increase in the number of heads sustaining less and less fertilization (Fig. 15). This sequence of out-cross pollen deposition considers the effect of a single insect as it forages on a ramet. The observed distribution of fertilization per head is the product of many such visits and therefore the singular effect must be multipled by the frequency of pollinator visits. Further variability in fertilization success between heads is a function of initial levels of out-cross pollen on the

Figure 15

Distribution of percentage of flowers fertilized per head. The cross-hatched area represents the 156 zero values that indicate a total lack of successful pollinations.


330
300
200
100
0
FREQUENCY
0
9.15
18.30
27.45
36.60
45.74
54.89
64.04
73.19
82.35
% FERTILIZED / HEAD

beetle. Size and purity of actual pollen loads are dependent on the beetle's preening efficiency and fidelity. Overall fertilization potential is decreased because only 55% of pollen grains are viable (Werner et al. 1980). The number of pollen grains needed to affect fertlization is another unknown variable.

Several factors may be responsible for the large number of heads experiencing a complete lack of fertilization. This "zero fertilization" class comprises 11% of total heads sampled (Fig. 14). The complete complexing of stigmatic lines by geitonogamous or interspecific pollen transfer is one possibility. All visitors utilizing S. canadensis as a food source may contribute. The most probable explanation of the lack of fertilization within a head is the absence of pollinator visits. Perhaps these heads were the first to open in the clone. In this case pollinator response may lag until sufficient resource has been made available, and a lack of fertilization results. Similarly, the heads may have been the last to open in the clone. Pollinators would have abandoned the clone as resources (nectar and pollen) fell below the average expected for the population as a whole.

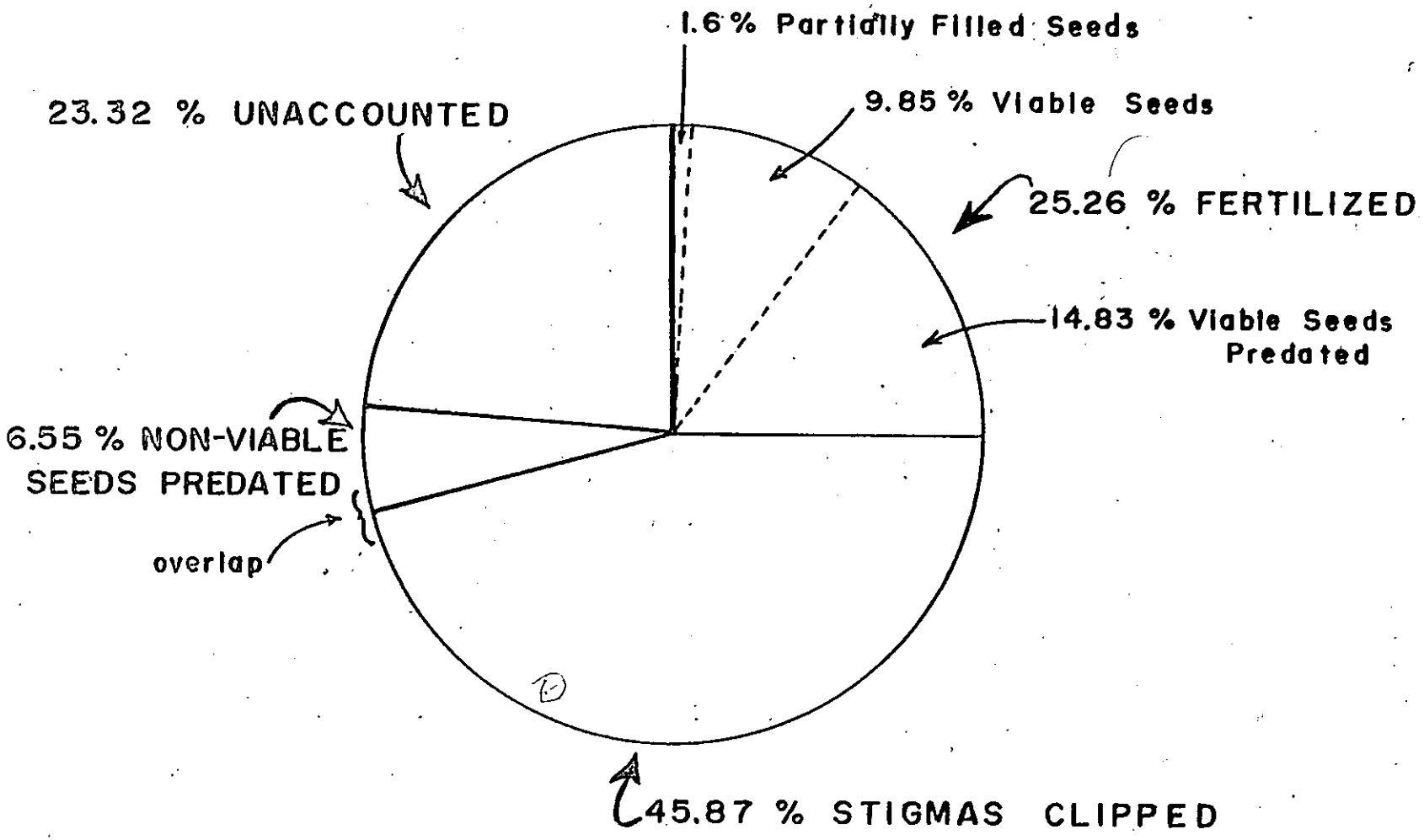
In this discussion of Chauliognathus foraging behaviour, I was not attempting to establish the presence of a special "co-evolved" plant-pollinator system. Solidago canadensis, like most other insect pollinated composites, is a generalist with respect to pollinators.

Dense colonies, extended flowering times, and aggregated heads allow for successful exploitation of many pollinator types, regardless of their particular foraging behaviour or energetic requirements. The generalist nature of goldenrod guarantees pollination success in any habitat that supports pollinators. The key to fertilization success in S. canadensis revolves around the long presentation time of each stigma and the head as a whole, permitting exposure to multiple pollinator visits.

To summarize the above functions Figure 16 considers the fate of flowers within a head. The values represent means for the entire spectrum of clone sizes. Of all the flowers within a head, an average of 25% were successfully fertilized and 75% were not. Of the 75% not fertilized, 45% had their stigmas removed by Epicauta and 7% were destroyed by the early instar larvae of Coleophora. This scheme does not identify the fate of 23% of the flowers that never formed seeds. This unaccounted portion may actually be larger than 23% since there is overlap between clipping and predation. I think this large proportion of unfertilized flowers reflects the general lack of pollinators for Solidago canadensis on Cayler Prairie. Paucity of pollinators, even in self-compatible plants, has been indicated as a major determinant of low seed-set (Barrett 1980, Platt et al. 1974). Secondly potential seed production could also be reduced by redundant (geitonogamous or interspecific) pollen spread that

Figure 16

Diagramatic representation of a 'generalized' head indicating the fate of its flowers. The values represent overall percentage means for the entire sample of clones. The extent of overlap between non-viable predation and stigma clipping is unknown.


1.6% Partially Filled Seeds
23.32 % UNACCOUNTED
9.85 % Viable Seeds
25.26 % FERTILIZED
14.83 % Viable Seeds Predated
6.55 % NON-VIABLE SEEDS PREDATED
overlap
45.87 % STIGMAS CLIPPED

pre-empts the stigmatic surfaces from legitimate pollinations.

2. Optimal Inflorescence (Head) Structure.

The adaptive nature of a plant's floral display has been investigated in numberous studies (Willson and Rathcke 1974, Willson and Price 1977, Stephenson 1979 and Schemske 1980). Evolution of an "optimal" inflorescence size may result from selection pressures such as attraction of pollinators (Janzen 1971c), probability of fruit set (Stephenson 1979), sexual constraints (Willson and Price 1977), and seed predation (Janzen 1971b). In the Compositae, the "unit of attraction" is the head (Burtt 1961), and as such is the level at which selection will act. Analogous to size is inflorescence structure. Burtt (1977) states that the "first important step in the diversification within the capitulum was, most probably, the restriction of the peripheral flowers to a female role, producing a capitulum that is functionally protogynous". He could not rationalize, however, why there would be peripheral female flowers if the plant is self-incompatible. Why should there be peripheral female flowers if they can not be pollinated by geitonogamous pollen? I believe the high predation rates experienced during the flowering stage, rather than a response to

pollination success, has produced this pattern within the head. Predation results from two sources: stigma clipping and ovule predation. Both act preferentialy on the disc flowers. Combined predation destroys 80% of the disc flowers and only 39% of the ray flowers. Of the 4.6 disc flowers per head, less than one would escape predation from these sources, while 6.5 of the 10.7 ray flowers per head would be available for fertilization. Ray flowers therefore will form the majority of seeds produced by each head. Sexually, disc flowers in the male phase function as pollen parents in future cross-fertilization acts. Disc flowers also produce nectar that, together with pollen, are the pollinator attractants. An optimal compromise would limit the number of disc flowers per head to balance pollen and nectar demands with predation pressure in the flowering phase. This balance would produce the maximum number of seeds per head, while still generating pollen to fertilize other flowers of a different genotype. Has there been a shift to reduce the number of disc flowers with increasing floral predation? On Cayler Prairie, S. canadensis heads actually do have many fewer disc than ray flowers. The validity of this hypothesis would have to tested by investigating other S. canadensis populations in habitats experiencing different intensities of floral predation and correlating predation to disc flower production within a head.

3. Seed Predation.

Root (1975) states that "herbivores are more likely to find and remain on host plants that are more concentrated (i.e., they grow in pure, large, and/or dense patches)". This "trapping" ability (Root 1973) of host patches depends on stand size, stand purity, and host plant requirements of the herbivore. In particular, specialist herbivores, i.e. those with a restricted host range, will show the strongest link with concentrated resources. Larvae of Coleophora spp. studied, are part of a group within the genus described as either mono- or oligo-phagous, feeding exclusively on Solidago and/or Aster (McDunnough 1956). Douwes (1968) found that the ovipositing female of the monophagous moth Cidaria albulata L. (Geometridae) was more efficient at finding host plants when the plants were aggregated into clumps. Also the female flew shorter distances between landings and changed directions more often near clumps, increasing the chances of finding a host plant. These changes in behaviour were stimulated by host plant odour. As a result these moths spent a minimum amount of time in areas with few host plants, and they accumulated near patches of their host plant.

The mobility of the herbivore will also determine the intensity of patch size response. Sharp, Parks and Ehrlich (1974) found no correlation between larval host plant distribution and butterfly distribution. Most species were

large, mobile butterflies that were capable of sampling resources over extensive areas. The only two exceptions in this study were two small, less mobile "blues" (Lycaenidae). Their movements were restricted to areas that contained their oviposition host plants. This localized habitat selection was more delimited when the host plants were patchily distributed. Coleophora spp. adults are very small and, like the "blues", are probably relatively weak fliers. This would tend to confine them to a restricted search area.

Since Root (1973,1975) proposed the "resource concentration hypothesis" many studies, mostly agricultural, have confirmed its importance as a factor regulating insect populations. Root (1973) and Tahvanainen and Root (1972), found that the flea beetle Phyllotreta cruciferae, which feeds exclusively on crucifers, had consistantly higher densities in large pure stands. Other Phyllotreta spp. with broader host ranges were able to colonize smaller plots and thus dampen the "concentration" response, although larger monospecific stands were always colonized more successfully than diverse stands (Root 1973, Cromartie 1975). Host specific sap-feeders of the salt marsh grass, Spartina patens, also responded in a density-sensitive manner. Of the twelve species of sap-feeders sampled nine had significantly greater densities in larger than smaller patches (Raupp and Denno 1979).

Since the mobile stage must locate the host, it is the ovipositing female Coleophora adult that establishes the population response to resource density. Colephora females can discriminate between patch sizes when ovipositing, demonstrating the resource concentration effect. The response appears to be enhanced by differential mortality of the larvae. Larvae in large clones enjoy higher survival rates due to a more reliable resource. The pattern of resource use by the larvae requires that they move between heads searching for viable seed. The more variation in this critical resource, the longer the search time required and the greater their exposure to predators. Due to their size and limited mobility, the larvae are most likely confined to the ramet on which they hatched. The patterns of larval survival are further reinforced by the within clone, i.e. ramet to ramet, variation in the seed-set per head. Larval mortality rates are likely determined by this resource variability within the colonized ramet. This resource tracking within clones could have generated the observed ramet to ramet differences in predation intensity.

Enhanced survival with increased resource density and predictability was also encountered by Ralph (1977), who studied the seed-sucking bug, Oncopeltus fasciatus, a specialist herbivore of Asclepias (milkweed). Variation in resource density, in this case reproductive plants, accounted for 63% ($r=0.798$) of the variation in nymphal

survival. The pattern of events was similar: dense populations of Asclepias were colonized by ovipositing females more than sparse populations. This was followed by a higher mortality of nymphs on sparse resource patches. Ralph (1977) believes this differential mortality was probably due to lower milkweed pod encounter rate and higher predation.

Another component of the "resource concentration hypothesis", affecting efficiency of host plant detection, is the vegetational diversity or "texture" of the surrounding community (Root 1975). In natural communities the effect of diversity must be considered in addition to density or size of resource patch. Both are determinants in shaping the observed response of the herbivore. Phyllotreta cruciferae colonized monocultures of cultivated collards (Cruciferae) more than those interplanted with tomatoes and tobacco (Tahvanainen and Root 1972). The chemical stimuli given off by these non-host plants interfered with the beetle's ability to locate its host. Tahvanainen and Root hypothesized that the background noise generated by the presence of non-host plants conveyed an "associational resistance" to plants growing in diverse natural vegetation. Cromartie (1975) confirmed this predicted outcome by showing decreased colonization by three collard specialists when plants were interspersed throughout diverse meadow vegetation. Bach (1980a,b) showed that the specialist striped cucumber beetle,

Acalymma vittata, maintained consistently higher populations (10-30 times greater, Bach 1980b) in cucumber monocultures as compared to polycultures (mixtures of cucumber and corn). Greater abundances in monocultures were caused by higher reproductive rates and longer tenure times (Bach 1980a). Bach (1980b) asserts diversity rather than density is the factor controlling herbivore abundances.

Solidago canadensis clones not only differ in size but in the degree to which they are associated with conspecifics and other species. Associational resisitance in this case has been translated into "what effect does proximity to, and density of, conspecifics have on discovery rate?". Many single ramet clones clustered together may be as "apparent" to their specialist herbivore as a large isoated clone. Vandermeer (1974) found that as isolation of individual plants, measured as distance to nearest conspecific neighbours, becomes greater percent seed predation decreases. This indirectly supports the goldenrod response: isolation from conspecifics by interspersion within the complex matrix of species found in Cayler Prairie decreases detection and the resultant predation. The predation pattern reflects seed-set response to these physical parameters.

The single flowering ramet clones, although rich in potential resources (seeds), were not always colonized by Coleophora. A few single ramet clones suffered no

predation at all. The probability of finding such a sparse patch would be small, especially if oviposition attraction is governed by the concentration of host plant odour (Douwes 1968, Ralph 1977), or if flight capability is limited. The smallest Asclepias stand Ralph (1977) monitored was also never colonized. It was by-passed by the searching Oncopeltus. Background noise (odour and/or visual cues) produced by the surrounding vegetation would also interfere with discovery of isolated individuals.

Although the size of the patch was the most important cue considered in the selection of oviposition sites, its correlation with ovule predation was small. Patch size accounts for little of the overall variation in early predation rate. Recently, several studies have shown great variation in pre-dispersal seed predation within single populations (Hare 1980, Janzen 1975, Moore 1978a,b). Moore (1978a) has documented that individual plants differed significantly in the intensity of seed predation, and these differences were maintained over time. The susceptibility of an individual was based on microhabitat, concentrations of toxic compounds and parasite load of the seed predators (Moore 1978b). It is conceivable that some of the differences in predation levels encountered between clones reflected an individual's (i.e. clone) consistant susceptibility to predation, rather than differences based solely on patch size. An example of such a mechanism might be genotypic differences in amount of toxins.

Several other factors may complicate the resource concentration response in Coleophora. Predators and parasites of Coleophora larvae may themselves show the resource concentration effect, removing a larger proportion of larvae at higher densities. This would dampen the apparent response of Coleophora. No measure was made of mortality inflicted by predators. Coleophora spp. utilize other species of Solidago, and perhaps even Aster. The presence of these alternate hosts, as well as their density and dispersion in relation to monitored clones could modify the moth's response by lessening dependency on S. canadensis. Again any detectable response to patch size would be reduced (Cromartie 1975, Root 1975). The six congeners and numerous Aster spp. might act as stepping stones between clones, negating any benefit accrued by isolation. If the suite of host plants differ in their acceptability as larval food, oviposition preference of the female may reflect this suitability in addition to the relative abundance of the resource (Chew 1977).

A plant's response to changes in density may itself alter some aspect of the morphological cue used by the female for oviposition. Density would then only secondarily regulate predation intensity (Bach 1980b). Thompson and Price (1977) showed the number of larvae/gram of umbel of the parsnip webworm Depressaria postinacella (Oecophoridae) was 50% higher on isolated parsnip plants (Umbelliferae) than high density plants. At lower

densities the plant had more unopened umbels, which are the oviposition sites, available over a longer period of time than high density plants. Isolated plants also had larger umbels which could support more larvae. The intensity of predation was governed by the plastic response of the plant to density rather than density as such. Resources available to Solidago may vary with location (microhabitat) as well as with clone size and density. This in turn may affect some physical determinant of ovipostion peference. Changes in plant morphology as a function of density may also complicate the patch size response in Coleophora. Ovipostion criteria are unknown for Coleophora.

Coleophora adults exploit a different resource (probably nectar and/or pollen) than the larvae. Thus adults must evaluate and choose a resource (seeds) for their relatively immobile larvae that has not yet developed and is unsuitable for themselves. The female must oviposit in clones and specifically on ramets that will provide adequate and acceptable food for her progeny. How does the female assess a clone or ramet for potential seed production? Does she directly assess the quality of the bud somehow or does she assess some variable that determines amounts of seed set? If the latter is true, possible cues signalling potential seed-set are floral patch size, pollinator activity, and presence of Epicauta. To a certain degree pollinator activity is correlated with floral pattch size. Increased patch size attracts more

visitors over time, which increases amount of seed available, and decreases variablity in seed-set between heads. The proximal cue for attraction to large clones, and hence greater seed predation, could therefore be pollinator activity. Zimmerman (1980b) has also suggested intensity of pre-dispersal seed predation is strongly linked with pollinator activity, but only when pollinators themselves are limiting to seed-set.

Coleophora adults may also be repulsed by the presence of Epicauta, or its inflicted damage. If the female feeds on nectar and/or pollen she could be sensitive to the absence of stigmas and not oviposit in those heads which have sustained high clipping damage. There is a negative correlation between the percentage of stigmas clipped per head and the percentage of flowers predated per head (rho=-0.1943), which suggests this type of avoidance. This negative correlation could also explain the positive correlation between floral predation and seed-set. More data on how and where Coleophora females oviposit are needed to verify this idea.

The basic natural history of Coleophora spp. is unknown. Many factors affecting its population levels must be known in order to quantify its habitat selection, both with respect to resource concentration and associational resistance. Knowledge of host-finding, colonization and patch tenure times, ovipostion site constraints, egg-laying pattern (number and dispersion), mobility of larvae and

their predation losses, and use of alternate hosts are crucial when testing these hypotheses (Dethier 1959, Young 1979). Root (1975) has also suggested dominant plants in late successional communities that form naturally concentrated, persistant patches would find less value in associational resistance. He proposes greater individual resistance and/or tolerance to herbivore attack via defense mechanisms such as hairs, spines and elaboration of various toxins, as alternative escape forms.

4. Conclusion

Assessing reproductive fitness or success is difficult when organisms utilize both sexual and asexual methods of reproduction. In plants with these dual reproductive modes, fitness can not simply be equated to the quantity of seeds produced and released, as is the case in totally sexual plants (Zimmerman 1980b). Another difficulty inherent in the study of clonal plants is that the vegetative portion itself has a dual nature. It can function as a reproductive as well as a vegetative (e.g. storage) structure. This latter role may determine competitive ability. Vegetative growth is an alternative resource sink that may in turn determine ultimate fitness by edging out competitors (Cody 1966).

Each type of reproduction contributes to the fitness

of an individual genotype in contrasting and complementary ways. Once established, vegetative reproduction enables the genotype to saturate a hospitable environment. It represents a relatively fast, low risk method of local expansion (Abrahamson 1975, Harper 1967). By spreading multiple, genetically-identical copies over space, the probability of survival over long time periods increases (Cook 1979, Sohn and Policansky 1977, Williams 1975). This mode of reproduction is particularily important when a new area is colonized and/or population density is sparse (Abrahamson 1979, Barrett 1980, Holler and Abrahamson 1977). The relative importance of asexual reproduction becomes evident when the community is temporally or spatially closed to seedling establishment (Putwain, Machin and Harper 1968, Thomas and Dale 1975).

The seed on the other hand acts as a dispersal unit, permitting increase over broad geographical regions, but with associated high risks (i.e. high mortality inflicted by many sources) (Harper 1977). Aside from the purely numerical increase, the sexual function also releases new genetic combinations that enable colonization of new, different habitats. Genetic survival beyond the finite clonal life is thereby ensured (Williams 1975).

The realization of this potential increase hinges on the availability of safe-sites. For a seed a safe-site is an area providing necessary stimuli and conditions for germination and shielding it from specific hazards such as

predators (Harper 1977). On Cayler Prairie safe-sites are very rare due to the very dense vegetation cover (Werner 1979). Therefore the probability of a seed reaching a potential safe-site depends on the total seed production of the clone and dispersability of the seed (Werner 1979). Since there is no reason to suspect different clones in the same area have different dispersal capacities, successful location and colonization of safe-sites is dependent on the absolute number of seeds a clone produces and releases (Green and Palmbald 1975, Moore 1978a). Availability of safe-sites may be a principal limiting factor for seedling establishment in closed communities (Barrett 1980, Putwain et al. 1968). Competition for safe-sites also delineates the ultimate community structure (Harper 1977, Werner 1979).

Increased clone size via vegetative growth increases the potential number of seeds that can be produced. In S. canadensis, floral patch size also determined pollination frequency and seed-set. Increasing size marginally increased seed-set per head. Concomitantly, larger clones suffered higher pre-dispersal seed predation per head. Therefore larger clones had proportionally fewer seeds per head escaping intact than small clones. Pre-dispersal seed predation reduces the absolute number of seeds that will be released by all clones, but the dispersal process and pattern will be unchanged (Harper 1977). Predation before dispersal will therefore decrease the probability a given

site will be colonized by a seed (Janzen 1971b).

The focal point of this discussion revolves around the net benefit accrued to large clones by virtue of their increased head, or ramet production. Proportionally greater predation intensities are more than balanced by increased ovule production. Larger clones ultimately produce more seeds, and hence retain a higher probability of locating a safe-site. The potential proliferation of clones that reach large size can therefore be maintained, when compared to smaller clones.

Literature Cited

Abrahamson, W.G. 1975. Reproductive strategies in dewberries. Ecology 56:721-726.

-----. 1979. A comment on vegetative and seed reproduction in plants. Evolution 33:517-519.

Aikman, J.M. and R.F. Thorne. 1956. The Cayler Prairie: An ecological and taxonomic study of a northwest Iowa prairie. Proc. Iowa Acad. Sci. 63:177-200.

Augspurger, C.K. 1980. Mass-flowering of a tropical shrub (Hybanthus prunifolius): Influence on pollinator attraction and movement. Evolution 34:475-488.

Bach, C.E. 1980a. Effects of plant diversity and time of colonization on an herbivore-plant interaction. Oecologia 44:319-326.

-----. 1980b. Effects of plant density and diversity on the population dynamics of a specialist herbivore, the striped cucumber beetle, Acalymma vittata (Fab.). Ecology 61:1515-1530.

Barr, A.J., Goodnight, J.H., Sall, J.P., Blair, W.H. and D.M. Chilko. 1979. SAS User's Guide. 1979 Ed. SAS Institute. Raieigh. NC.

Barrett, S.C. 1980. Sexual reproduction in Eichhornia crassipes (water hyacinth). II.Seed production in natural populations. J. Appl. Ecol. 17:113-124.

Beattie, A.J. 1971. A technique for the study of insect-borne pollen. Pan-Pac. Entomol. 47:82.

-----, Breedlove, D.E. and P.R. Ehrlich. 1973. The ecology of the pollinators and predators of Frasera speciosa. Ecology 54:81-91.

Beaudry, J.R. and D.L. Chabot. 1959. Studies on Solidago L. IV.The chromosome numbers of certain taxa of the genus Solidago. Can. J. Bot. 37:209-228.

Breedlove, D.E. and P.R. Ehrlich. 1968. Plant-herbivore coevolution: Lupines and lycaenids. Science 162:671-672.

Borror, D.J. and D.M. DeLong. 1971. An Introduction to the Study of Insects. 3rd ed. Holt, Rinehart and Winston. N.Y.

Bradbury, I.K. 1973. The Strategy and Tactics of Solidago canadensis L. in abandoned pastures. Ph.D. Dissertation, University of Guelph, Guelph, Ontario.

----- and G. Hofstra. 1977. Assimilate distribution patterns and carbohydrate concentration changes in organs of Solidago canadensis during an annual developmental cycle. Can. J. Bot. 55:1121-1127.

Burtt, B.L. 1961. Compositae and the study of functional evolution. Trans. Proc. Bot. Soc. Edinburgh 39:216-232.

-----. 1977. Aspects of diversification in the capitulum. In: The Biology and Chemistry of the Compositae. Eds. V.H. Heywood, J.B. Harborne and B.L. Turner. Academic Press, N.Y.

Carpenter, F.L. 1976. Plant-pollinator interactions in Hawaii: Pollination energetics of Metrosideros collina (Myrtaceae). Ecology 57:1125-1144.

Charnov, E.C. 1976. Optimal foraging: Attack strategy of a mantid. Amer. Natur. 110:141-151.

Chew, F.S. 1977. Coevolution of pierid butterflies and their cruciferous foodplants. II.The distribution of eggs on potential foodplants. Evolution 31:568-579.

Cody,M.L. 1966. A general theory of clutch size. Evolution 20:174-184.

Cohen, J. and P. Cohen. 1975. Applied Multiple Regression / Correlation Analysis for the Behavioral Sciences. John Wiley and Sons. N.Y.

Conover, W.J. 1971. Practical Nonparametric Statistics. John Wiley and Sons Inc. N.Y.

Cook, R.E. 1979. Asexual reproduction: A further consideration. Amer. Natur. 113:769-772.

Cromartie, W.J.Jr. 1975. The effect of stand size and vegetational background on the colonization of cruciferous plants by herbivorous insects. J. Appl. Ecol. 12:517-533.

Cronquist, A. 1955. Phylogeny and taxonomy of the Compositae. Amer. Midl. Nat. 53:478-511.

Cruden, R.W. and S. Hermann-Parker. 1979. Butterfly pollination of Caesalpinia pulcherrima, with observations on a psychophilous syndrome. J. Ecol. 67:155-168.

Dethier, V.G. 1959. Food-plant distibution and density and larval disperal as factors affecting insect populations. Can. Entomol. 91:581-596.

Douwes, P. 1968. Host selection and host finding in the egg-laying female Cidaria albulata L. (Lep.Geometridae). Opusc. Entomol. 33:233-279.

Draper, N.R. and H. Smith. 1966. Applied Regression Analysis. John Wiley and Sons. N.Y.

East, E.M. 1940. The distribution of self-sterility in the flowering plants. Proc. Amer. Phil. Soc. 82:449-518.

Faegri, K. and L. Van Der Pijl. 1971. The Principles of Pollination Ecology. 2nd ed. Pergamon Press. N.Y.

Fernald, M.L. 1950. Gray's Manual of Botany. 8th ed. American Book Co. N.Y.

Frankie, G.W., Opler, P.A. and K.S. Bawa. 1976. Foraging behaviour of solitary bees: Implications for outcrossing of a neotropical forest tree species. J. Ecol. 64:1049-1057.

Free. J.B. 1960. The behaviour of honeybees visiting flowers of fruit trees. J. Anim. Ecol. 29:385-395.

-----. 1966. The pollinating efficiency of honey-bee visits to apple flowers. J. Hort. Sci. 41:91-94.

Fryxell, P.A. 1957. Mode of reproduction of higher plants. Bot. Rev. 23:135-233.

Gentry, A.H. 1978. Anti-pollinators for mass-flowering plants?. Biotropica 10:68-69.

Gibbons, J.D. 1971. Nonparametric Statisical Inference. McGraw-Hill Book Co. N.Y.

Gleason, H.A. and A. Cronquist. 1963. Manual of Vascular Plants of Northeastern United States and Adjacent Canada. Van Nostrand Reinhold Co. N.Y.

Grau, J. 1977. Astereae - a systematic review. In: The Biology and Chemistry of the Compositae. Eds. V.H. Heywood, J.B. Harborne and B.L. Turner. Academic Press. N.Y.

Green, T.W. and I.G. Palmbald. 1975. Effects of insect seed predators on Astragalus cibarius and Astragalus utahensis (Leguminosae). Ecology 56:1435-1440.

Hare, J.D. 1980. Variation in fruit size and susceptibility to seed predation among and within populations of the cockebur, Xanthium strumarium L. Oecologia 46:217-222.

Hartling, L.K. and R.C. Plowright. 1978. An investigation of inter- and intra-inflorescence visitation rates by bumblebees on red clover with special reference to seed set. Proc. IVth Int. Symp. on Pollination, Md. Agric. Exp. Sta. Spec. Misc. Publ. 1:457-460.

Harper, J.L. 1967. A Darwinian approach to plant ecology. J. Ecol. 55:247-270.

-----. 1977. Population Biology of Plants. Academic Press. N.Y.

Hawthorn, W.R. and P.D. Hayne. 1978. Seed production and predispersal seed predation in the biennial composite species, Artium minus (Hill) Bernh. and A. lappa L. Oecologia 34:283-295.

Heinrich, B. 1975. Energetics of pollination. Ann. Rev. Ecol. Syst. 6:139-170.

-----. 1976. The foraging specializations of individual bumblebees. Ecol. Monogr. 46:105-128.

-----. 1979a. "Majoring" and "minoring" by foraging bumblebees, Bombus vagans: An experimental analysis. Ecology 60:245-255.

-----. 1979b. Resource heterogeneity and patterns of movement in foraging bumblebees. Oecologia 40:235-245.

----- and P.H. Raven. 1972. Energetics and pollination ecology. Science 176: 597-602.

Hill, G.R. and W.J. Platt. 1975. Some effects of fire upon a tall grass prairie plant community in northwestern Iowa. In: Prairie: A Multiple View. Ed. M.K. Wali. University of North Dakota Press. Grand Forks, ND.

Holler, L.C. and W.G. Abrahamson. 1977. Seed and vegetative reproduction in relation to density in Fragaria virginiana (Rosaceae). Amer. J. Bot. 64:1003-1007.

Horsfall, W.R. 1943. Biology and control of common blister beetles in Arkansas. Arkansas Agric. Exper. Station Bull. 436:3-55.

Janzen, D.H. 1971a. Euglossine bees as long-distance pollinators of tropical plants. Science 171:203-205.

-----. 1971b. Seed predation by animals. Ann. Rev. Ecol. Syst. 2:465-492.

-----. 1971c. Escape of Cassia grandis beans from predators in time and space. Ecology 52:964-979.

-----. 1975. Intra- and interhabitat variations in Guazuma ulmifolia (Sterculiaceae) seed predation by Amblycerus cistelinus (Bruchidae) in Costa Rica. Ecology 56:1009-1013.

Johnson, L.K. and S.P. Hubbell. 1975. Contrasting foraging strategies and coexistence of two bee species on a single resource. Ecology 56:1398-1406.

Leppik, E.E. 1970. Evolutionary differentiation of the flower head of the Compositae II. Ann. Bot. Fennici 7:325-352.

-----. 1977. The evolution of capitulum types of the Compositae in the light of insect-flower interaction. In: The Biology and Chemistry of the Compositae. Eds. V.H. Heywood, J.B. Harborne and B.L. Turner. Academic Press. N.Y.

Levin, D.A. and W.W. Anderson. 1970. Competition for pollinators between simultaneously flowering species. Amer. Natur. 104:455-467.

----- and H.W. Kerster. 1974. Gene flow in seed plants. Evol. Biol. 7:139-220.

McDunnough, J.H. 1956. On the Aster- and Solidago-feeding species of the genus Coleophora in Nova Scotia (Lepidoptera, Coleophoridae). Amer. Mus. Novit. 1777:1-20.

Meeuse, J.D. 1959. Beetles as pollinators. Biologist 42:22-32.

Messina, F.J. 1978. Mirid fauna associated with old-field goldenrods (Solidago: Compositae) in Ithaca, N.Y. N.Y. Entomol. Soc. 86:137-143.

Moore, L.R. 1978a. Seed predation in the legume Crotalaria. I.Intensity and variability of seed predation in native and introduced populations of C. pallida Ait. Oecologia 34:185-202.

-----. 1978b. Seed predation in the legume Crotalaria. II.Correlates of interplant variability in predation intensity. Oecologia 34:203-223.

Moore, R.P. 1973. Tetrazolium staining for assessing seed quality. In: Seed Ecology. Ed. W. Heydecker. Penn. State University Press. University Park, Pa.

Morse, D.H. 1977. Foraging of bumble bees: The effect of other individuals. N.Y. Entomol. Soc. 85:240-248.

Mulligan, G.A. and J.N. Findlay. 1970. Reproductive systems and colonization in Canadian weeds. Can. J. Bot. 48:859-860.

Nie, N.H., Hull, C.H., Jenkins, J.G., Steinbrenner, K. and D.H. Bent. 1975. Statistical Package for the Social Sciences. 2nd ed. McGraw-Hill Book Co. N.Y.

Owen, D.B. 1962. Handbook of Statistical Tables. Addison-Wesley Pub. Co. Reading, Mass.

Platt, W.J. 1975. The colonization and formation of equilibrium plant species associations on badger disturbances in a tall-grass prairie. Ecol. Monogr. 45:285-305.

-----, Hill, G.R. and S. Clark. 1974. Seed production in a prairie legume (Astragalus canadensis L.). Oecologia 17:55-63.

Price. P.W. 1975. Insect Ecology. John Wiley and Sons. N.Y.

Primack, R.B. and J.A. Silander Jr. 1975. Measuring the relative importance of different pollinators to plants. Nature 255:143-144.

Putwain, P.D. Machin, D. and J.L. Harper. 1968. Studies in the dynamics of plant populations. II.Components and regulation of a natural population of Rumex acetosella L. J. Ecol. 56:421-431.

Pyke, G.H. 1978a. Optimal foraging: Movement patterns of bumblebees between inflorescences. Theor. Pop. Biol. 13:72-98.

-----. 1978b. Optimal foraging in bumblebees and coevolution with their plants. Oecologia 36:281-293.

-----. 1979. Optimal foraging in bumblebees: Rule of movement between flowers within inflorescences. Anim. Behav. 27:1167-1181.

-----, Pulliam, H.R. and E.L. Charnov. 1977. Optimal foraging: A selective review of theory and tests. Quart. Rev. Biol. 52:137-154.

Ralph, C.P. 1977. Effect of host plant density on populations of a specialized seed-sucking bug, Oncopeltus fasciatus. Ecology 58:799-809.

Raupp, M.J. and R.F. Denno. 1979. The influence of patch size on a guild of sap-feeding insects that inhabit the salt marsh grass Spartina patens. Environ. Entomol. 8:412-417.

Rogers, C.E. 1978. Sunflower moth: Feeding behavior of the larva. Environ. Entomol. 7:763-765.

Root, R.B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: The fauna of collards (Brassica oleracea). Ecol. Monogr. 43:95-124.

-----. 1975. Some consequences of ecosystem texture. In: Ecosystem Analysis and Prediction. Ed. S. Levin. Soc. Ind. Appl. Math. Philadelphia, Pa.

Salisbury, N.E. and J.C. Knox. 1969. Glacial land forms of the big kettle locality, Dickinson County, Iowa. Development Ser. Rep. 6 Iowa State Advisory Board for Preserves, Des Moines.

Schaal, B.A. 1978. Density dependent foraging on Liatris pycnostachya. Evolution 32:452-454.

Schemske, D.W. 1980. Evolution of floral display in the orchid Brassavola nodosa. Evolution 34:489-493.

Schmidt, J. 1980. Pollinator foraging behavior and gene dispersal in Senecio (Compositae). Evolution 34:934-943.

Sharp, M.A., Parks, D.R. and P.R. Ehrlich. 1974. Plant resources and butterfly habitat selection. Ecology 55:870-875.

Sheldon, J.C. and F.M. Burrows. 1973. The dispersal effectiveness of the achene-pappus units of selected Compositae in steady winds with convection. New Phytol. 72:665-675.

Silander, J.A. Jr. 1978. Density-dependent control of reproductive success in Cassia biflora. Biotropica 10:292-296.

Skvarla, J.J., Turner, B.L., Patel, V.C. and A. S. Tomb. 1977. Pollen morphology in the Compositae and in morphologically related families. In: The Biology and Chemistry of the Compositae. Eds. V.H. Heywood, J.B. Harborne and B.L. Turner. Academic Press. N.Y.

Smith, A.P. and J.O. Palmer. 1976. Vegetative reproduction and close packing in a successional plant species. Nature 261:232-233.

Sohn, J.J. and D. Policansky. 1977. The costs of reproduction in the mayapple Podophyllum peltatum (Berberidaceae). Ecology 58:1366-1374.

Sokal, R.R. and F.J. Rohlf. 1969. Biometry. W.H. Freeman. San Francisco.

Stephenson, A.G. 1979. An evolutionary examination of the floral display of Catalpa speciosa (Bignoniaceae). Evolution 33:120-1209.

Tahvanainen, J.O. and R.B. Root. 1972. The influence of vegetational diversity on the population ecology of a specialized herbivore, Phyllotreta cruciferae (Coleoptera: Chrysomelidae). Oecologia 10:321-346.

Thomas, A.G. and H.M. Dale. 1975. The role of seed reproduction in the dynamics of established populations of Hieracium floribundum and a comparison with that of vegetative reproduction. Can. J. Bot. 53:3022-3031.

Thompson, J.N. and P.W. Price. 1977. Plant plasticity, phenology, and herbivore dispersion: Wild parsnip and the parsnip webworm. Ecology 58:1112-1119.

Thomson, J.D. 1980. Skewed flowering distributions and pollinator attraction. Ecology 61:572-579.

----- and R.C. Plowright. 1980. Pollen carryover, nectar rewards, and pollinator behavior with special reference to Diervilla lonicera. Oecologia 46:68-74.

Vandermeer, J.H. 1974. Relative isolation and seed predation in Calliandra grandiflora, a Mimosaceous legume from the highlands of Guatemala. Biotropica 6:267-268.

Waddington, K.D. 1979. Divergence in inflorescence height: An evolutionary response to pollinator fidelity. Oecologia 40:43-50.

Waldbauer, G.P. 1968. The consumption and utilization of food by insects. Adv. Insect Physiol. 5:229-288.

Waser, N.M. 1978a. Interspecific pollen transfer and competition between co-occuring plant species. Oecologia 36:223-236.

-----. 1978b. Competition for hummingbird pollination and sequential flowering in two Colorado wildflowers. Ecology 59:934-944.

Werner, P.A. 1979. Competition and coexistance of similar species. In: Topics in Plant Population Biology. Eds. O.T. Solbrig, S. Jain, G.B. Johnson and P. Raven. Columbia University Press. N.Y.

-----, Bradbury, I.K. and R.S. Gross. 1980. The biology of Canadian weeds. 45. Solidago canadensis L. Can. J. Plant Sci. 60:1393-1409.

----- and W.J. Platt. 1976. Ecological relationships of co-occuring goldenrods (Solidago: Compositae). Amer. Natur. 110:959-971.

Williams, G.C. 1975. Sex and Evolution. Princeton University Press. Princeton, New Jersey.

Willson, M.F. and R.I. Bertin. 1979. Flower-visitors, nectar production, and inflorescence size of Asclepias syriaca. Can. J. Bot. 57:1380-1388.

----- and P.W. Price. 1977. The evolution of inflorescence size in Asclepias (Asclepiadaceae). Evolution 31:495-511.

----- and B.J. Rathcke. 1974. Adaptive design of the floral display in Asclepias syriaca L. Amer. Midl. Natur. 92:47-57.

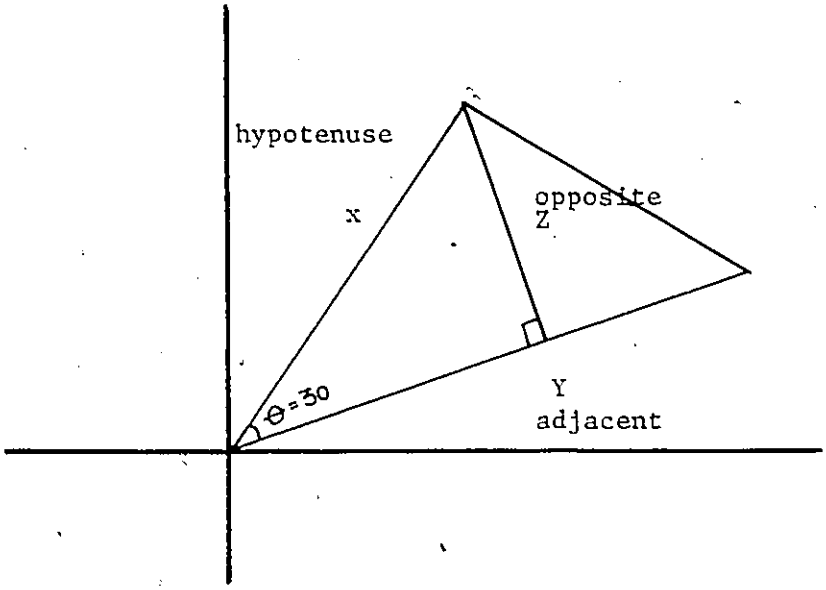
Young, A.M. 1980. Evolutionary responses by butterflies to patchy spatial distributions of resources in tropical environments. Acta Biotheor. 29:37-64.

Zimmerman, M. 1980a. Reproduction in Polemonium: Competition for pollinators. Ecology 61:497-501.

-----. 1980b. Reproduction in Polemonium: Pre-dispersal seed predation. Ecology 61:502-506.

Appendix 1. Program used to calculate the area occupied by each clone.

```
 5   DIM X (12)
10   FOR I=1 TO 12: INPUT X(1): NEXT 1
15   FOR I=1 TO 12: J=I+1:IF J=13 THEN J=1
20   AR=AR+(0.25* X(I) X(J)):NEXT
25   PRINT "AREA OF DODECAGON=AR"
```



* $\sin\theta = \frac{\text{opposite}}{\text{hypotenuse}} = \frac{Z}{x}$

$x \sin 30 = Z = x\ (0.5)$

Area= ½ base · height

= ½ Y · Z

= ½ Y (0.5 x)

= ½ (0.5 xY)

= 0.25 xY

Appendix 2. Nested Anova for the arcsine transformed percentage fertilized/head.

SOURCE	DF	SUM OF SQUARES	MEAN SQUARE	F VALUE	PR > F	R^2	CV
Model	123	160.42791637	1.30429200	9.08	0.0001	0.46404	39.0057
Error	1290	185.29539101	0.14363984				
Corrected Total	1413	345.72330738					

SOURCE	DF	TYPE I SS	F VALUE	PR > F
CLONE	18	84.83568254	32.81	0.0001
POSITION(CLONE)	105	75.59223383	5.01	0.0001

Appendix 3. Nested Anova for the arcsine transformed percentage fertilized/head.

SOURCE	DF	SUM OF SQUARES	MEAN SQUARE	F VALUE	PR > F	R^2	CV
Model	123	160.42791637	1.30429200	9.08	0.0001	0.46404	39.0057
Error	1290	185.29539101	0.14363984				
Corrected Total	1413	345.72330738					

SOURCE	DF	TYPE I SS	F VALUE	PR > F
Number of flowering ramets/clone	1	46.62188331	324.57	0.0001
Percentage of stigmas clipped/head	1	25.98348302	180.89	0.0001
CLONE	17	16.46447540	6.74	0.0001
POSITION(CLONE)	104	71.35807463	4.78	0.0001

VITA AUCTORIS

Born	June 23, 1954. Windsor, Ontario.
1972	Graduated Riverside High School, Windsor, Ontario.
1976	B.Sc. (Hon.), University of Guelph, Department of Botany and Genetics, Guelph, Ontario.
1981	M.Sc., University of Windsor, Department of Biology, Windsor, Ontario.