THE BIONOMICS OF *Wyeomyia smithii* (COQUILLETT), THE PITCHER PLANT MOSQUITO (DIPTERA: CULICIDAE: SABETIINI)

A Thesis

Presented To

The Department of Entomology

Faculty of Agriculture

The University of Manitoba

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

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August 1971

ABSTRACT

THE BIONOMICS OF *Wyeomyia smithii* (COQUILLETT), THE PITCHER PLANT MOSQUITO (DIPTERA: CULICIDAE: SABETHINI).

Several aspects of the biologies of both the mosquito, *Wyeomyia smithii*, and its habitat, *Sarracenia purpurea*, were investigated. The life cycle of *S. purpurea* is discussed in detail. A general survey of plants found in a Manitoba bog is presented.

The leaves of the pitcher plant which form the sole habitat of *W. smithii* begin growth in late summer, become dormant through the winter, and emerge in the spring. The leaves mature by early summer and persist until the following summer (12 to 15 months).

The geographic distribution of *S. purpurea* in North America is illustrated. Records for the plant in northern Manitoba are new. Other invertebrates utilizing the pitcher plant as a habitat in Manitoba are *Blaesoxipha fletcheri* (Aldrich), *Endothenia daeckeana* Krt., *Exyra rolandiana* Grt., the water mite *Anoetus gibsoni* (Nesbitt), and aphid of the genus *Macrosiphum*.

Respiration rates and feeding rates of diapausing and non-diapausing larvae of *W. smithii* were studied. No differences in respiration rates were detectable between diapausing and non-diapausing larvae; differences were noted in feeding and the uptake of ^{137}Cs between the two groups of larvae.

Diapause occurs in third instar larvae of this species, when first instar and early second instar larvae are reared at daily photoperiods of less than 14 1/2 to 15 hours light. At long-day photoperiods (16 1/2L:7 1/2D or more),

development proceeds uninterrupted. Diapause is terminated in third instar larvae by long-day photoperiods. Larvae can be held in diapause for several months at short-day photoperiods (14L:10D or less), particularly if the temperature is lowered (10°C). In field populations at this latitude, diapause is terminated about mid-April, although development is delayed for about a month by suboptimal temperatures. At 50°15'N. Lat., diapause-inducing photoperiods (less than 14 1/2L:9 1/2D) occur during the first week in August. All larvae hatching after this date would diapause in the third instar.

Studies of cold tolerance and supercooling in *W. smithii* showed that the larvae were unable to survive sub-zero temperatures for long periods. Less than 50% survived when held at -5°C for eight weeks. The larvae did not supercool below -5°C. Snow cover is shown to be instrumental in the winter survival of *W. smithii* and provides sufficient insulation to prevent ground temperatures from becoming critically low. The average survival of overwintered larvae was 50%.

Observations on field populations of *W. smithii* showed that at this latitude only one generation occurs each year. Continuous generations are possible in the laboratory, but in the field this species is environmentally univoltine due to the limitations of photoperiod and temperature. The developmental period of *W. smithii* is restricted to about two months (June to August). Development times, seasonal changes, and duration of the various life stages are discussed and illustrated. Several aspects of the biology of each life stage is presented. Population transfer from leaves of the previous year's growth to leaves of the current year's growth is examined.

W. smithii adults were found to be autogenous and ovarian development is described and illustrated. Mating behavior of adults, both in the field and in the laboratory, was found to be similar.

ACKNOWLEDGEMENTS

To my Supervisor, Dr. R. A. Brust, I wish to express my most sincere thanks for his encouragement and many helpful suggestions. His constant interest and support in this programme provided me an excellent opportunity for studies both in the field and in the laboratory. To my colleague, Mr. Allen Wiens, my sincere thanks for his companionship and assistance during the many field trips we shared.

I am indepted to Dr. A. Stone, Systematic Entomology Laboratory, United States Department of Agriculture for assistance on the taxonomy of *Wyeomyia smithii*. My thanks for species identification to Dr. H. J. Teskey (Diptera), and Dr. M. MacKay (Lepidoptera), Entomology Research Institute, Canada Department of Agriculture, Ottawa, and Dr. P. Barker (Acarina), Stored Products Entomologist, Canada Department of Agriculture, Winnipeg.

I also take this opportunity to express my appreciation to Mr. Walter Chunys, Atomic Energy of Canada Ltd., for his invaluable assistance in the field. To Mr. A. Reimer, Meteorologist, Atomic Energy of Canada Ltd., who so willingly supplied much of the meteorological data, and to Dr. J. Guthrie, Director, Environmental Control Section, Atomic Energy of Canada, Ltd., for his cooperation and assistance, I am deeply grateful. I would also like to thank the many people of Canada Department of Forestry for the use of the facilities at Red Rock Lake, and for a most enjoyable summer spent there.

To my examiners, Dr. S. C. Jay, Department of Entomology, and Dr. G. Robinson, Department of Botany, my sincere gratitude for their constructive criticisms and suggestions. To Dr. Steven Smith, Department of Biology, University of Waterloo, sincere thanks for his assistance and advice given so freely during the period of study.

I am also indebted to Miss Janet Schubert for her assistance and all-round good humor in the laboratory. My thanks also to Mr. J. Serger, Technician, Department of Entomology, for his assistance in many of the technical aspects of this study. To Miss Judy Emmett, who assisted my wife in the typing of this thesis, I am deeply grateful.

To my wife, Lorraine, I express my most sincere thanks and appreciation for her unending patience, encouragement, and assistance, which prevailed throughout this period of study.

This research has been supported by grants from the National Research Council, which I gratefully acknowledge.

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Chapter 1

INTRODUCTION

Insectivorous plants represent an interesting point of contact between the plant and insect worlds. In most instances, the relationship that exists in plant-insect inquilines is that both the plant and the insect benefit or the insect benefits at the expense of the plant. In rare instances, this relationship is reversed and the plant becomes the sole benefactor.

These unusual plants, found in both the Old and New Worlds, are capable of attracting, trapping, and digesting a broad spectrum of insects and small vertebrates. There are, however, some insects which utilize the plants as either a food source, directly or indirectly, or as a habitat for part or all of their life cycle. One such relationship is that which exists between the pitcher plant mosquito, *Wyeomyia smithii* (Coq.) and the Purple Pitcher Plant, *Sarracenia purpurea* L.

W. Smithii is a rather obscure and little understood species which, as far as is known, inhabits only the leaves of the pitcher plant, *S. purpurea* (Barr, 1958). Pitcher plants have long attracted attention because of their carnivorous habit and a striking dissimilarity to any other plants found in this country. Although the pitcher plant has been known for some 370 years, having been first published as a sketch by an unknown author in 1601, (Lloyd, 1942), no mention of *W. smithii* appears in the literature until the beginning of the twentieth century. Since that time, relatively few authors have published on *W. smithii*. One of the main reasons for this is

undoubtedly the fact that this is a non-biting, weak flying species and has offered no threat to man either as a pest species or as a disease vector.

Larvae of *W. smithii* and of the chironomid, *Metriocnemus knabi* (Coq.), were discovered in the leaves of the pitcher plant, *S. purpurea*, near Kenora, Ontario in 1968. Several other locations were subsequently located and investigations were begun in the spring of 1969, with the purpose of expanding the bionomics of the species involved.

A review of the literature showed that aside from the generalized account of the life history worked out by its discoverer, Dr. J. B. Smith, in 1901-1902, little had been added since that time. Recent literature still refers to these early works as primary sources. Practically no field studies had been conducted and even laboratory work has been very limited. Smith (1902) observed that the larvae overwinter, encased in the ice of the pitcher leaves, but since that time no one has studied the stage (instar) of overwintering, cold tolerances, survival, or the environmental factors involved. No work has been done on diapause in this species. The number of generations per year were undetermined, although the species has proved to be multivoltine. In addition, mating, oviposition, ovarian development, and activity rhythms have received little attention. The relationship of the mosquito to the plant had not been studied. In short, there is still a lot of basic biological research which could be done on this species.

Through May, 1969 to January, 1971, a series of field studies was carried out in which several aspects of the bionomics of this species were examined. Meteorological records were kept with the purpose of attempting to understand some of the climatic factors relating to *W. smithii* and its habitat. In turn, this data was related to population fluctuations, winter

survival, diapause, and activity rhythms.

In conjunction with field studies, controlled laboratory experiments were carried out in order to substantiate the field results and to isolate certain factors regulating the population in order that the effects could be more clearly demonstrated.

Because *W. smithii* is associated with *S. purpurea*, it was necessary to look at the biology of this plant as well. Observations of the life cycle, habitat, distribution, associated flora and fauna are dealt with in some detail as part of this study.

Chapter 2

LITERATURE REVIEW

Section A

A review of some of the pertinant literature relating to insectivorous plants, with special reference to the Sarracenians and their insect inquilines.

Throughout the world, from tropical swamp to upland marsh, some 450 species of carnivorous plants belonging to 15 genera, flourish, utilizing a curious array of devices to attract, capture, and digest small forms of animal life. Listings of the families, genus, number of species, and geographic distribution are given by Lloyd (1942) and by Wherry (1935). Typically these plants grow in soil that is wet and acid, usually deficient in nitrates and phosphates that the "normal" plant life requires (Salamun, 1970; Zahl, 1964; Jones, 1921; Lloyd, 1942; Cooke, 1882). Some carnivorous plants live above ground, in trees, for example, while others are actually submerged.

Zahl (1961) states that the highly specialized leaf of the carnivorous plants utilizes three basic methods for capturing food. (1) The "steel trap" type which clamps its leaf halves together on its prey. Examples of this type are *Dionaea musciplula,* the "Venus Fly Trap" and the aquatic plant, *Aldrovana vesiculosa.* (2) The "fly paper" type, exemplified by *Drosera*, the "Sundews", of which there are some 90 species, mire their prey on a sticky secretion. (3) The "pit-fall" type in which the prey tumbles into a cupped pool of liquid consisting of water, bacteria, and digestive secretions.

The families Sarraceniaceae and Nepenthaceae are representatives of this latter type. All three types of trapping methods are found among the six carnivorous genera found in North America.

The family Sarraceniaceae is made up of three genera: *Sarracenia*, *Chrysamphora* and *Heliamphora* (Wherry, 1935). While commonly referred to as "pitcher plants", they should not be confused with the true pitcher plants, the Nepenthacaea, which have their curious pitchers suspended from the leaves on stalks (Zahl, 1964). The histology, biology, and morphology of these plants are dealt with in detail by Lloyd (1942), Darwin (1899), Macfarlane (1893, 1889), Bower (1889), and by Cooke (1882). Of the three genera, only *Sarracenia* and *Chrysamphora* occur in the northern hemisphere. The five species of *Heliamphora* are found only in South America and are not discussed here.

The genus *Chrysamphora* (or *Darlingtonia*) is monotypic, its single species *Darlingtonia californica* occurs locally in Oregon and California (Zahl, 1961; Lloyd, 1942; Wherry, 1935). It has been reported in British Columbia, Canada, but the northern limits of the range are not known (Krajina, 1968). Known locally as the "Cobra plant", it attains a height of two to three feet, and is unique in its appearance, with large motely domes and fish-like appendages (Lloyd, 1942). Insects are lured to the opening by a strong odor and once having entered, must continue forward, eventually slipping into the plant's internal pool (Zahl, 1961; Lloyd, 1942, Macfarlane, 1892). Unlike *Sarracenia*, the liquor of *Darlingtonia* contains only bacteria to absorb the nutrient matter (Zahl, 1961, Lloyd, 1942).

In the genus *Sarracenia*, nine species are recognized, all of which occur in North America (Wherry, 1935). Early records of this genus date back as far as 1576 (Lloyd, 1942). Like *Darlingtonia*, the Sarracenians

utilize an attractive nectar secretion to lure insects to the opening. Once there, downward pointing hairs direct the victims' movements to the liquid. The prey loses footing on the smooth conducting inner surface of the pitcher and drops into the fluid (West, 1965; Jones, 1935, Macfarlane, 1893; Cooke, 1884; Riley, 1874).

Any insect entering the mouth of the pitcher stands a good chance of becoming a victim rather than a visitor. The success of these pitchers as traps is attested to by the vast array of organisms one finds within the leaves. Wray and Brimley (1943) give a detailed account of trap species found in the pitcher plants of North Carolina. Similar studies were carried out by Swales (1969) and Judd (1959) on *Sarracenia purpurea*, and by Philip (1952) and Goodnight (1940) on *S. flava*. These studies showed that in addition to small frogs, toads, lizards, spiders, slugs, and snails, representatives of almost every order of insect can be found in these traps.

The nature of the digestive liquid contained within the leaves of these plants has been the subject of much study as has the mode of action of the enzymes therein. For a more complete review of this aspect of Sarraceniaceae physiology, see Plummer (1966), Lloyd (1942), Macfarlane (1893, 1889), and Cooke (1882).

The relationship of insects and other organisms to the Sarracenians, is not, however, confined to the status of trap and victim. They are, like many other plants, dependent on insects for pollination and the flowers are physiologically and structurally adapted to encourage, if not to enforce, cross fertilization (Jones, 1935, 1908). Among the most frequent visitors are ants, bees, butterflies, moths and pollen-eating beetles.

The microhabitat provided by the leaves of the pitcher plant has been invaded by several species of animals which make use of the rich food supply

to be found there. The degree of adaptation of these inquilines varies but in some instances, the association between insect and plant, insofar as the insect is concerned, is obligatory. In some cases, the organism feeds directly on the plant, while in others it feeds on the trapped material. Table 1 gives a list of the known recorded insect inquilines of the Sarraceniaceae. Several species of spiders are known to frequent the mouth of the pitchers and, in some cases, actually utilize the pitcher structure (Zahl, 1961; Lloyd, 1942; Jones, 1935).

Since the relationship of *W. smithii* to *S. purpurea* is of prime concern in this study, the literature is reviewed separately in Section B.

Table 1

Summary of the known insect associates of the Sarraceniaceae.

Insect Species	Plant Associate	Reference
Lepidoptera		
Olethreutes daeckeana (*O. hebesana*) Kearfott	*S. minor* (on flower, stamens, ovaries)	Jones, 1908, 1935 Kearfott, 1907
Papaipema appassionata Harvey	*S. flava* (in Rhizomes) *S. purpurea* (in Rhizomes)	Jones, 1908, 1935, 1916 Bird, 1903
Exyra rolandiana Grt.	*S. purpurea* (on/in leaves)	Jones, 1904, 1907, 1921, 1935 Judd, 1957
Exyra rigengsii Riley	*S. flava* (on/in leaves)	Jones, 1904, 1907, 1908, 1921, 1935
Exyra semcroces Gm.	*S. rubra* (on/in leaves) *S. minor* (on/in leaves) *S. drumondii* (on/in leaves) *S. sledgi* (on/in leaves) *S. psittacina* (on/in leaves)	Jones, 1907, 1921, 1935 Riley, 1874
Archip parallela Rob.	*S. minor* (on/in leaves) *S. purpurea* (on/in leaves)	Jones, 1908 Judd, 1959

Table 1 (continued)

Insect Species	Plant Associate	Reference
Diptera		
Sarcophaga sarraceniae Riley	*S. variolaris* (on detritus in leaf)	Jones, 1904, 1935 Aldrich, 1916
S. utilis	*S. purpurea* (on detritus in leaf)	Riley, 1874 Wray and Brimley, 1943
S. rileyi	*S. rubra* (on detritus in leaf)	
S. celarata	*S. flava* (on detritus in leaf)	Jones, 1908
S. jonesi	*S. purpurea* (on detritus in leaf)	Judd, 1959
Fletcherimyia fletcheri (Ald.)		
Metriocneumus edwardsi Jones	*Darlingtonia californica* (on detritus in leaf)	Jones, 1916
Metriocnemus knabi Coq.	*S. purpurea* (on detritus in leaf)	Knab, 1905 Jones, 1916 Judd, 1959
Wyeomyia smithii (Coq.)	*S. purpurea* (in water, within leaf)	Smith, 1901-1904 Dyar, 1901 Jones, 1916 Wray and Brimley, 1943 Judd, 1959
Wyeomyia haynei Dodge	*S. purpurea* (in water, within leaf)	Dodge, 1947

Table 1 (continued)

Insect Species	Plant Associate	Reference
Sciara macfarlanei *(Neosciara)* Jones	*S. flava* (drier detritus) *S. rubra* (drier detritus) *S. sledgi* (drier detritus) *S. drummondii* (drier detritus) *S. minor* (drier detritus)	Jones, 1935, 1920 Wray and Brimley, 1943
Dohrniphora venusta Coq.	*S. flava* (drier detritus)	Jones, 1918
Botanbia darlingtoniae Jones	*Darlingtonia californica* (drier detritus)	Jones, 1916
Acarina:Anoetidae		
Aneotus gibsoni *(Zwickia)*(Nesbitt)	*S. purpurea* (in leaves)	Nesbitt, 1954 Hunter et al, 1964
Histiostoma sp.	*S. purpurea* (in leaves)	Judd, 1959
Macroseuis biscutatus	*S. minor* (in leaves)	Muma and Denmark, 1967
Hymenoptera		
Isodontia philadephicus Lep.	*S. flava* (nest in leaves)	Jones, 1904
Polistes fuscatus *pallipes* Lep.	*S. purpurea* (nest in leaves)	Bernon, 1969

Section B

A review of the literature pertaining to *Wyeomyia smithii* (Coq.).

W. smithii is a member of a basically tropical group of mosquitoes known as the Sabethini (Dyar, 1928). Apart from three old world genera, this large group is almost exclusively neotropical and all are basically plant breeders, utilizing places where small amounts of water collect.

The genus *Wyeomyia* is primarily a South American genus, but its range is extended to include northeastern U.S.A. and Canada in the case of *W. smithii*, and the distribution apparently coincides with the range of its host plant, *S. purpurea* (Wherry, 1935; Mattingly, 1962). *W. smithii* is unique among the Sabethini in that the larvae overwinter, encased in the ice-cores of the pitcher plant leaves and can apparently withstand recurrent periods of freezing and thawing.

The presence of *W. smithii* in pitcher plants was probably observed long before it was recorded. It seems unlikely that a plant with a history like *S. purpurea* would have insect associates for hundreds of years without discovery. It is possible that the larvae were mistaken for some other species. In 1900, J. Turner Blakeley brought to the attention of J. B. Smith in late November the fact that in the pitcher plants at Lahaway, New Jersey, there were mosquito larvae. Smith first assumed these to be *Culex pungens (pipiens)*, a species common to the area, which breeds in many areas and overwinters as an adult (Smith, 1901). Interest was generated when it was found that the species overwintered as larvae, "frozen" in the ice of the pitchers. Early accounts of the rearing of these larvae and preliminary investigations are given by Smith (1901, 1902) and Howard (1902).

D. W. Coquillett subsequently revealed that this was a new species, *Aedes smithii* (Coquillett, 1901; Dyar, 1901; Smith, 1902). By 1904 its accepted

taxonomic name became *Wyeomyia smithii* (Coq.).

Smith (1904) published a review of his research on this species, including the material from his earlier publications of 1901 and 1902. In this paper, Smith presents the basic life history as it occurs in the field. Briefly stated, the life history as described by Smith is as follows:

> "The insect overwinters in the larval stage, freezing and thawing as often as need be during the season. It pupates in late May and becomes adult a week or ten days later. Eggs are laid in leaves singly or in small groups; fastened to the sides or floating on the surface. The summer broods mature in about a month and there are probably three if not four series; but the broods overlap so much that the breeding is practically continuous. Late in the season the adults select new leaves for oviposition even if they are yet dry."

Smith found that the number of larvae per pitcher varied between 2 and 20 and that their rate of development varied considerably among individuals. The pupal period averaged about eight days. The adults do not take a blood meal and since few adults were seen, it was assumed that adult activity took place mainly at night.

E. G. Mitchell (1905) noticed that in plants collected in South Carolina, larvae differed slightly from those described by Dyar (1901). Mitchell (1905) reported that the speciments she examined had four anal gills (two being small and difficult to see in alcohol specimens) whereas those described by Dyar had only two. It was this point that later led Dodge (1947) to describe a new species.

Owen (1937) conducted some experiments on the tolerance of larvae and pupae to freezing. Results indicated that the larvae were killed by a temperature of -14°C if held at that temperature for longer than two hours. Pupae were even more sensitive to low temperature.

Roth (1946) showed that the three species of *W. vanduzeei* Dyar and Knab,

W. mitchelli (Theobald), and *W. smithii* (Coquillett) could be separated by the female genitalia.

Experiments by Bick and Penn (1947) showed that fourth instar larvae of *W. smithii* were capable of surviving up to 192 hours of experimental drought. They suggested that this would be important to the survival of the larvae, since the pitcher leaves would be subject to occasional drying.

Dodge (1947) described a new species, *Wyeomyia haynei*, from the pitcher plants of South Carolina. Having read the paper by Mitchell (1905) and on the examination of both living specimens and specimens kept in alcohol, Dodge was confinced that there were two separate species. Dodge suspected that the range of the two species was limited by their host plants; *haynei* being restricted to *S. purpurea venosa* and *smithii* to *S. purpurea gibbosa*. He states, however, that further collection should be made before the exact range can be determined.

Following Dodge's (1947) description of *W. haynei*, southern records of *Wyeomyia* from pitcher plants have often been uncritically assigned to that species (example, Weatherbee and Arnold, 1947, 1948). However, confirmed identifications to support this claim have not been forthcoming and a collection of larvae from pitcher plants from North Carolina, within the putative range of *haynei*, were found to be *smithii* (Smith, pers. comm.). The distribution of the two species therefore remains a moot point but it seems certain that all Canadian material is assignable to *smithii*.

Jenner (1951) was the first to demonstrate the photoperiodic control of larval diapause in *W. smithii*. Short photoperiods (less than 15 hours light/24 hours) was effective in maintaining the diapause state while long photoperiods (greater than 15 hours/24 hours) promoted pupation.

Haufe (1952), in a study of the mosquitoes of the Goose Bay, Labrador region, noted the presence of *W. smithii* larvae in leaves throughout the summer and this record represents one of the more northern points of distribution.

A laboratory culture of *W. smithii* was established by Price (1958), permitting the investigation of several aspects of the biology. The females were autogenous (ovarian development without a blood meal) for the first ovarian cycle and matured an average of 51.5 eggs. The adults did not require carbohydrate food for oogenesis but such supplements increased longevity and vigor. Ovipositing females preferred a water surface to wet filter paper, in contrast to observations of egg-laying under field conditions (Smith, 1902). This species was also colonized by Wallis and Frempong-Boadu (1967). Their observation also indicated that eggs were laid on the fluid surface rather than at the sides of the containers.

Another report by Price (1958a) describes a unique 'monster' embryo in 15 of 1570 eggs. However, it was not considered to be of any ecological or biological significance.

In a series of studies of the Byron Bog in southwestern Ontario, Judd (1959), correlated the events of the life cycle of both *W. smithii* and *S. purpurea*.

A study and description of the egg of *W. smithii* was given by Barr and Barr (1969) as well as a review of the studies of the Sabethini eggs. They also presented evidence for the eggs being laid while moisture was present.

Swales (1969) in a study on both the victims and inquiline of the pitcher, *S. purpurea*, theorizes on the possible reasons for the survival of the larvae in a digesting media. One possibility is the presence of active enzyme inhibitor with those organisms which inhabit the pitcher fluid,

although no evidence has been forthcoming to support this theory. (This author found that *Aedes atropalpus* (Coq.) survived and developed without any apparent damage in filtered pitcher plant fluid.)

Bacteria is believed to play only a minor role, however, they should also be considered. Enzyme action is thought to occur from within rather than externally, entering through the various body openings and attacking the drowned insects' softer parts from the inside. In the case of the fluid habitants, Swales suggests that perhaps the epithelium of the gut is resistant to the plant enzymes so that when ingested along with food, they cause no harm. A second possibility suggested that the pH of the insect gut may neutralize the enzyme, rendering it inactive.

Some aspects of the cohabitation of *S. purpurea* by *W. smithii* and *M. knabi* were looked at by Buffington (1970). Although *W. smithii* and *M. knabi* appear to be initially in competition with one another, the former is basically a filter feeder, while the latter browses on the detritis. Thus they are inhabiting two distinct niches. This niche segregation permits cohabitation through differential utilization of the same food source.

Hudson (1970) in an attempt to relate autogeny to mouth parts, found that morphologically at least, *W. smithii* appeared to be capable of taking a blood meal. However, no blood feeding nor host seeking behavior has been observed.

Smith and Brust (1971) showed that overwintering (diapausing) larvae did not survive for more than 60 days when held at a constant temperature of -5°C. Larval diapause was terminated by long-day photoperiods, the critical photoperiod of an Ontario population being 14 1/2 hours of light per diem. All females were autogenous with high fecundity. Oogenesis

was found to be precocious lending support to the supposition that the species is non-blood-sucking.

Chapter 3

METHODS AND MATERIALS

Location of Study

The program of research was carried out on four bogs--three in Manitoba and one in Ontario (Fig. 1). *S. purpurea* and *W. smithii* were abundant in all four bogs. The Ontario location (Fig. 1, Area 1) was a lake-edge bog, southeast of Kenora, 17 miles off Highway 71. Area 2 was in the FIG (Field Irradiated Gamma) area, a restricted zone for ecological studies and part of a large bog located on the Atomic Energy of Canada Ltd. property, four miles north of Manitoba Highway 211. Area 3 was located at Canada Department of Forestry plot, situated seven miles east of the junction of Highways 44 and 311, near Telford, Manitoba. Area 4 was a more northern site, located 0.5 miles down the Radio Range Road, 9.5 miles north of The Pas, Manitoba. These bogs were selected because it was hoped that their large size would confer a degree of immunity from disturbances due to prolonged sampling programmes.

The bog located in the FIG Area (Pinawa Bog) was studied in more detail than the others. A detailed map is presented in Figure 2 as well as an aerial view in Figure 3.

Sampling and Field Observations

Sampling and field observations were carried out on a more or less regular basis during the summers (May to November) of 1969 and 1970 and on an infrequent basis during the winters (November to April) 1969-1970

and 1970-1971. Actual collection dates are indicated in the collection summary table in Appendix A.

The sampling technique involved the selection of leaves and their contents at random. The plant leaves (pitchers) were removed and placed in pans together with a small amount of sphagnum. Each pan held between 25 to 35 leaves, and from two to four pans were collected. Not all of the leaves were removed from any given plant (except in the case where it was done to determine the average leaf size per plant and the number of leaves per plant), nor was preference shown for any one area within the bog. New leaves (current year's growth) were kept separate from old leaves (previous year's growth).

In the laboratory at Winnipeg, several leaves were selected at random, the contents of each emptied, and the number and instar of larvae recorded. Other records taken included the number of pupae and the sex, number and sex of the pupal exuvia (classed as adults), number of eggs if present, and the leaf capacity (measured in total ml. of water each leaf was capable of holding). (See Appendix A.) The larvae, pupae, and pupal exuvia were preserved in 70% alcohol. In some instances, the eggs were retained for hatching and the results were recorded after ten days. The contents of the remaining sample of pitcher leaves were emptied, pooled, and the larvae and pupae used in experiments or for stock cultures.

Field observations were made of plant development, emergence of new leaves, occurrence of flowers, amount of leaf decay, and of adult mosquito activity. These observations were greatly aided by the use of both 35 mm. and 16 mm. photographic equipment.

Winter collections for determining winter survival of larvae were carried out in much the same manner, except leaves were taken from pre-

determined sites. The plants had been staked the previous fall to aid recovery when blanketed with snow. Leaves, with their frozen ice-cores were transported to the laboratory in styrofoam coolers. This prevented thawing while in transit, and insulated the larvae from unfavourably low air temperatures. Leaves were placed at 5°C to thaw, and the necessary measurements and counts carried out the following day.

Adult mosquitoes were also found and taken in the field during the summer. Those captured in flight were kept separate from those found resting within the pitchers. Once captured (via aspirator) adults were placed in 1" x 1" x 6" cages. The cages were made of acrylic plastic with fine cloth screening on two sides. The cages were then wrapped in moist paper towels thereby protecting the adults from desiccation while enroute to the laboratory. There they were counted, sexed, and dissected to determine the number of eggs and the stage of ovarian development. Presence of sperm in the spermatheca was also noted.

Observations were made of adult behavior and mating activity, and copulation under field conditions. The behavior of adults in the field was later compared with that in the laboratory. Observations were attempted at various times of the day to determine when adult activity was greatest.

Sex ratios of field populations were determined from pupae reared from samples of larvae collected from various locations.

A continuous daily record of the temperature at the level of the pitcher leaves (sphagnum temperature) was carried out from October 1, 1969 to October 18, 1970, using two Taylor* 7 Day (11" chart) temperature recorders. These were mounted in plywood boxes set on a staked platform, four feet above

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*Taylor Instrument Co. of Canada Ltd., Toronto, Canada.

the ground, as shown in Figures 4 and 5. The microhabitats in which the two recorders were located were slightly different. One was placed in a fairly open area; the other was in the shade, well sheltered by black spruce and tamarack. A malfunction in one of the Taylor instruments required its replacement by a Weksler** Type 6MRP with a 6" chart.

In addition to ground or plant temperatures, records were taken of air temperatures, rainfall, snowfall, snow depth, day length (Smithsonian Meteorological Tables, 1966), direction of prevailing winds from October, 1969 to October, 1970. A summary of this data is given in Appendix B.

An attempt was made to have *W. smithii* oviposit in artificial containers ("pitchers") in the field. For this purpose, various glass vials with openings of 23 mm., 16 mm., and 12 mm. (Fig. 6) were used. Some were set up with paper toweling liners on the inside. The vials (with and without liners) were filled from 3/4 to 4/5 full with distilled water. They were set into the sphagnum with about 1/2" of the vial showing above the surface (Fig. 7). These were checked periodically for eggs and larvae.

In addition to field studies on *W. smithii* and assessment of the plant species present in the Pinawa Bog (Area 2), and their distribution was carried out in the fall of 1969. The method used to determine the spacial distribution of the plant species was that of McGinnis (1934). Detailed observations were conducted on *S. purpurea*, in an attempt to understand the life cycle of this plant and its relationship to the biology and ecology of *W. smithii*.

Since the distribution of *S. purpurea* is poorly documented, especially its northern and western limits, inquiries were sent to herbaria, museums,

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**Weksler Instrument Corp., Freeport, N.Y., U.S.A.

universities, botanists, and other interested persons in Canada, U.S.A., and Mexico in an attempt to substantiate the potential range of this plant. This, it was felt, would give an indication as to the possible range of *W. smithii*, of which even less is known.

Laboratory Culture

Larvae were reared in shallow circular (2 cm. x 15 cm.) plastic pans containing approximately 100 cc. of distilled water. The diet per 100 larvae was as follows:

Tetramin* Fish Food "L" . . . . . 10 mg.

Tetramin* Fish Food "E" . . . . . 10 mg.

Ground commercial dog food . . . . . 25 mg.

Ground brewer's yeast . . . . . 10 mg.

Dried blood meal . . . . . 10 mg.

Later in the study, 25 mg. of ground turtle food and 25 mg. of ground dried daphnia were added to the above diet. The larval media was changed every two to four days, depending on conditions of the water. High mortality occurred whenever the water became foul. This situation was probably the results of over-feeding. Aeration was attempted but this did not seem to have any beneficial effects. Pans were washed in tap water (no soaps or detergents were used) and rinsed in distilled water before reusing. As experience was gained in handling of the cultures, the diet was mixed dry in bulk and used as required. It was wetted with distilled water and added to the cultures with an eyedropper, experience dictating the amount served to each pan. The amount offered was based on

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*TetraKraftWerke, West Germany

the food left from the previous feeding, the mortality, and the general overall appearance of the culture. This method gave high levels of survival (70%). Adults appeared large and healthy, and reproduction did not appear to suffer.

At each change, pupae, if present, were removed and placed in emergence cages. Since no standard rearing procedure for *W. smithii* has been developed, several emergence/mating cages were tried, and the one shown in Figure 8 proved to be best suited, being of simple construction, easy to manipulate, clean, and maintain. The construction of this cage is based on suggestions by Dr. A. Hudson, Entomological Research Institute, Ottawa.

The base of the emergence cage consists of a half gallon ice cream container cut to size (about 2 1/2"), with a hole in the top for a 4 oz. wide mouth glass jar. The hole is reinforced around the edge with black tape and the entire inside of the container is sprayed with flat black paint. The top portion of the cage is a 7" lamp chimney, open at both ends. Black plastic tape is wrapped around the outside (3/4 of the way up) to reduce the light. The top portion is covered with a cloth screen, held in place with an elastic band (Fig. 9). Adult diets of either apple, raisins, cotton soaked in honey, or sugar solution can be placed on this screen and covered with a plastic petri dish. The inside of the chimney has two or three strips of masking tape on which the adults can rest, although no preference was shown for these areas and adults appeared to rest with equal east on either the glass or the tape.

The complete top of the cage can be lifted (including the pupal jar) so that observations can be made on pupal mortality, egg deposition, and hatching without disturbing or losing the adults. Adults are allowed to emerge, mate and oviposit within these cages. Newly emerged larvae were removed every two to four days, and placed in the plastic rearing pans.

Dead adults and pupal exuvia were also removed. Live pupae are returned to the jars in fresh distilled water. Approximately 75 to 100 pupae or adults were kept in each cage. Adults can easily be transferred from cage to cage with the aid of an aspirator and the upport portion of the cage (lamp chimney) can be lifted for inspection with little or no loss of adults. Adults are reluctant to fly and will do so only when disturbed. When disturbed, they fly upwards into the top of the chimney.

Stock cultures were kept in constant temperature B.O.D. incubators (Crelab, Model 1212, temperature differential ±.45)* (Fig. 10). The relative humidity fluctuated, but appeared to be sufficiently high to prevent disiccation of the adults. When open pans of water were present in the incubators, the humidity was often above 85 to 90%. For non-diapausing larvae, cultures were maintained at 27±1°C, with a photoperiod of 18 hours light/6 hours dark, which allowed development to proceed uninterrupted. Both fluorescent and incandescent light was used with similar results. For diapausing larvae, or for holding diapausing field-collected larvae, a temperature of 20±1°C and a photoperiod regime of 12L:12D were used. Under these conditions, larvae would develop to, but not progress beyond, the third instar. Field-collected diapausing larvae could be maintained at this temperature and photoperiod for several months. Diapausing larvae required much less food than non-diapausing ones.

Photoperiod and Diapause

In conjunction with the field studies, several laboratory investigations were carried out in order to study some of the factors effecting the population in the field. A major portion of this work was devoted to determining

*Climatic Research Equipment Ltd., Winnipeg, Manitoba

the control of diapause in this species. Investigations of the induction, maintenance, and termination of diapause were carried out using photoperiod as the controlling factor.

(i) Induction of diapause

Larvae used in diapause-induction experiments were taken from laboratory-reared cultures, maintained at 27±1°C/18L:6D. In order to determine the developmental stage(s) which respond to photoperiod and the photoperiod(s) which is capable of inducing diapause, the following experiments were conducted at 27±1°C.

1) Eggs kept at 18L:6D--larvae reared at various photoperiods.

2) Eggs and first instar larvae kept at 18L:6D--larvae (second and third instar) reared at various photoperiods.

3) Egg, first and second instar larvae kept at 18L:6D--subsequent stages at various photoperiods.

In preliminary experiments, field-collected larvae of unknown age were used but the results were not conclusive. Later experiments showed that the age of the larvae is important in diapause induction, and the age in days was unknown in field collections. Subsequent experiments were conducted with eggs and larvae taken from the laboratory colony kept at 27±1°C and 18L:6D.

During treatment, larvae were reared in 70 x 50 mm. glass crystalizing dishes containing about 75 ml. of distilled water. Larvae were fed the same diet as the stock cultures and the medium was changed every two to four days. At each change, the number of larvae, instar, number of pupae and sex were noted. Rearing was carried out in a water bath which was capable of maintaining a pre-set temperature within one-tenth of a degree in the water bath itself and within one-half a degree in the rearing dishes.

The water bath was sectioned into six compartments by using one-eighth

inch black plastic sheeting, held in place and made light-proof with sponge rubber weather stripping. (3/8" x 3/16") and metal-to-rubber household cement (Fig. 12). These sections extended to within 2 1/2" of the bottom of the bath (at least 3" below the water surface). The stainless steel lids of the sections were fitted with six volt miniature lamps and shielded with a plastic jar (Fig. 13). Each lamp was controlled individually using a variable rheostat and the photoperiods were controlled using 24-hour, clock driven electric timers. Temperature of the bath was maintained by four 250 watt-115-125 volt infra-red heat lamps controlled by a Micro Set Thermo Regulator*. A small electric agitator circulated the water within the tank, aiding in maintaining the temperature. The construction was designed to reduce the light leakage to a minimum (0.5 foot candles or about .01%) and appeared to be completely "dark" to the human eye. To limit any chance of reflection off the bottom from one section to the other, the water was dyed with food colouring. As an additional precaution, a black muslin cloth was draped over the top of the bath. The body of the bath was constructed of copper sheeting, insulated on the outside. The entire unit was fitted with a floor-length skirt of black plastic (Fig. 11). Each section held two 7" x 7" x 1" stainless steel pans. The pans were supported by styrofoam strips which acted as flotation devices. The water level in the bath was such that the pans floated about seven inches below the top of the bath (six inches from the light source). Each pan held three of the glass crystalizing dishes.

All experimental trials were conducted at 25±0.5°C, using the following photoperiods:

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*Precision Scientific Co., U.S.A.

10.0L:14.0D
12.0L:12.0D
14.0L:10.0D
14.5L: 9.5D
15.0L: 9.0D
15.5L: 8.5D
16.0L: 8.0D
16.5L: 7.5D
17.0L: 7.0D
18.0L: 6.0D

Induction of diapause was defined as a failure of the larvae to progress beyond the third instar stage after 40 days.

(ii) Diapause termination

Studies of the termination of diapause were also done. Diapausing larvae (third instar), either collected from the field or reared in the laboratory, were exposed to various photoperiods in an attempt to determine which photoperiod terminated diapause, and allowed development to continue. Pre-treatment consisted of holding larvae at 12L:12D and 20°C for a variable period of time. Larvae were then placed at the experimental photoperiods at 20°C.

Experiments were carried out in a variety of light boxes, some with incandescent lighting, others with fluorescent. No effort was made to analyze the type of lighting used or its effects. Larvae were reared (or held) prior to the experiment in plastic pans as outlined under culture methods. During the experimental period larvae were reared in 70 x 50 mm. glass crystalizing dishes, containing about 75 ml. of distilled water, plus larval diet. The medium was changed every two to four days. All stages were counted, and the pupae were sexed.

Records were kept on the number of larvae that molted to the fourth instar, and the number that pupated. Molting to the fourth instar was considered to be sufficient evidence of the termination of diapause.

Behavior of Diapause Larvae

(i) Feeding

In the initial rearings, it was noted that much more food remained in those pans containing diapausing larvae than in pans containing non-diapausing larvae. Although it is generally believed that the larvae of *W. smithii* feeds in the diapause state, it has not been confirmed. Therefore the following experiments were conducted to test if diapausing larvae feed.

Measurements were made in gut contents using a method developed by Dadd (1968). The ingestion of carbon particles is easily determined. Rates of ingestion were compared in three grounds of larvae: (1) Non-diapausing third instar reared at 18L:6D/27°C; (2) Diapausing third instar larvae collected from the field (January, 1971) and held at 12L:12D/20°C; (3) diapausing third instar reared at 12L:12D/20°C. Larvae were first starved for 48 hours in distilled water, then placed in rearing pans containing distilled water to which was added two to three drops of black drawing ink. One hundred larvae of each group were allowed to feed on this suspension for 25 days while kept at their respective photoperiods and temperatures. Larvae were inspected daily for five days, then at 10, 15, 20, and 25 days, and the presence of carbon in the gut noted. Ingestion rates were classified as A (up to 1/2 full), B (1/2 to 3/4 full), and C (3/4 to full).

To determine if ingestion rates (feeding) differed if larvae were fed a nutritive diet instead of inert material, larvae from each of the three test groups were starved for 48 hours, then fed on carbon particles for four days, and subsequently placed in distilled water containing a few drops of regular larvael diet. The subsequent replacement of the carbon particles in the gut tract by the food particles was noted. The boundary between the carbon and the food remained stable and no mixing of the gut contents occurred.

Larvae were inspected at 3, 6, 9, 12, and 24 hours after being placed in the nutritive media. The stages of carbon loss (or food uptake) were D (up to 1/2 replacement), E (1/2 to 3/4 replacement), and F (3/4 to full replacement).

Feeding rates were also compared using radiocesium (^{137}Cs) labeled dog food (Guthrie, 1969). One hundred diapausing third instar larvae collected in the field and held for two months at 12L:12D/20°C, and 100 non-diapausing third instar larvae reared in the laboratory at 18L:6D/27°C were compared. After a starvation period of 48 hours, larvae were placed in distilled water with the labeled dog food and allowed to feed for a period of 24 hours. A sample of 20 larvae were taken at each of the following times: 1, 3, 6, 12, and 24 hours. The larvae were washed four times in distilled water, placed on aluminum counting planchets and dried under infra-red lamps. The larvae were covered with a 1:10 solution of collodion in acetone, then counted on a Nuclear/Chicago Beta Counter. Differences in counts were interpreted as differences in feeding rates. Each larva was counted for 30 minutes (3 x 10 minutes).

Since ion exchange can occur through the anal papillae of mosquito larvae (see Clements 1963), a preliminary experiment was carried out to see if differences could be detected between diapausing and non-diapausing third instar larvae. Fifty larvae of each group were starved for 48 hours then placed in nutritive-free ^{137}Cs media and kept at 18L:6D/27°C, for 48 hours. A sample of 10 larvae were taken from each of the two groups at 3, 6, 12, 24, and 48 hours, and handled as before. Differences in counts were interpreted as difference in ionic uptake rates.

(ii) Respiration

Diapause is associated with a suppression of the rate of development

and of the metabolic rate, as measured by oxygen consumption (see Beck 1968). Experiments were conducted to determine whether differences are detectable in the respiration rates of diapausing and non-diapausing third instar larvae and whether these differences, if any, could be used to determine whether diapause had occurred.

Using a Gilson Differential Respirometer, groups of larvae were placed in the respirometer flasks along with 5 ml. of distilled water and 1 ml. of 5% KOH and a CO_2 absorber. Larval groups compared were:

(1) Diapausing third instar collected in the field and held at 12L:12D/20°C.

(2) Non-diapausing third instar collecting in the field and held at 18L:6D/27°C.

(3) Non-diapausing third instar reared at 18L:6D/27°C.

(4) Fourth instar collected in the field as third instar larvae and reared to fourth instar at 18L:6D/27°C.

(5) Fourth instar reared at 18L:6D/27°C.

(6) Second instar reared at 18L:6D/27°C.

The initial trial was run at 20°C, but subsequent trials were carried out at 25°C in a attempt to amplify the differences. Duration of the trials varied from 7 to 12 hours, and the number of larvae used per flask varied from 20 to 50. In each trial, equal numbers were used.

Once the system was closed to the external atmosphere, the larvae were allowed to equilibrate for one hour. Subsequently oxygen consumption was checked hourly. The results are expressed as microliters of oxygen/larvae/hour.

(iii) Survival at low temperature

An experiment was carried out to determine how long larvae could survive

at various sub-zero temperatures and how this information was related to the temperatures to which they were subjected in the field.

Larvae (field-collected diapausing larvae) were placed in small (3" x 4") styrofoam cartons (10 per carton--20 per temperature) containing about 25 ml. of distilled water. Experiments were doncuted at the following temperatures: 20°, 10°, 5°, -1°, -5°, -10°, -15°, -20°, and -25°C. In the first trial, larvae were pre-conditioned at 10°C for 2 days, at 5°C for 7 days, and at -1°C for 7 days prior to being placed at the sub-zero temperatures. The larvae were then thawed and inspected after 12 hours, 24 hours, 2 days, 3 days, 1 week, 2 weeks, 3 weeks, 4 weeks, 6 weeks, 8 weeks, and 10 weeks. Upon thawing, larvae were allowed to recover for 24 hours before survival was checked.

The above experiment was repeated using a longer pre-conditioning period:

20°C--12L:12D for 2 months.

10°C--12L:12D for 1 month.

5°C--12L:12D for 1 month.

Those placed at -5° had been kept at -1° for 1 day prior to treatment.

Those placed at -10° had been kept at -1° for 1 day, -5° for 1 day, prior to treatment.

Those placed at -15° had been kept at -1° for 2 days, -5° for 2 days, and -10° for 4 days prior to treatment.

Those placed at -20° had been kept at -1° for 2 days, -5° for 2 days, -10° for 2 days, and -15° for 1 day prior to treatment.

Those placed at -25° had been kept at -1° for 2 days, -5° for 2 days, -10° for 2 days, and -20° for 1 day prior to treatment.

A similar comparison was made with non-diapausing third instar larvae, except that the experiment was terminated after a period of 4 weeks.

(iv) Supercooling

In conjunction with the experiments on survival at low temperatures, comparisons of various larval groups were made to determine at what point freezing of the tissue actually occurs. Six groups of larvae were subjected to decreasing temperatures and their freezing points noted. Freezing point of the tissue was determined by attaching an individual larvae, previously dried for 3 to 5 minutes on blotting paper, to a bimetalic thermocouple using petrolium jelly as an adhesive. The larvae and thermocouple were immersed into a cooling bath of ethyl alcohol (ETOH) and dry ice (CO_2). The bath was operated at a temperature of -64°C. The rate of cooling, determined by three air spaces (Fig. 14: A_1, A_2, A_3), was 8°C and 12°C per minute. The temperature of the larvae was measured by a recording potieniometer (Fi.g 15). The freezing point was determined as the lowest recorded point reached prior to "peaking" caused by the heat of crystalization, which occurred as the larva tissue fluid froze.

The following groups of larvae were tested:

(1) Diapausing third instar--field-collected and held at 12L:12D/20°C for 3 months.

(2) Diapausing third instar--field-collected just prior to the experiment (29/12/70).

(3) Diapausing third instar--held at 12L:12D/20°C for 1 month, 12L:12D/10°C for 2 months, and 12L:12D/5°C for 1 month.

(4) Non-diapausing third instar--reared at 18L:6D/27°C.

(5) Second instar--reared at 18L:6D/27°C.

(6) Fourth instar--reared at 18L:6D/27°C.

(v) Temperature growth threshold

To assess the ability of third instar larvae to develop at various

temperatures, three groups of larvae were placed under long-day photoperiod (18L:6D) at 27°, 20°, 15°, 10°, and 5°C for 50 days. Larvae were checked periodically and the percent molting to fourth instar noted. Larval groups were: (1) Laboratory-reared diapausing third instar, reared at 12L:12D and 20°C; (2) Field-collected diapausing third instar, held at 12L:12D and 20°C; (3) Laboratory-reared non-diapausing third instar, reared at 18L:6D and 27°C.

Chapter 4

THE BIOLOGY OF *Sarracenia purpurea* L.

(i) Description

Observations of pitcher plants in Manitoba and Ontario were begun in May 1969 and terminated in February 1971. The plants are readily distinguished by a rosette of tubular shaped leaves, resembling pitchers, and vary in colour from pale green (in new leaves) to dark green with rich reddish-purple veins in mature leaves (Fig. 16). The pitchers attain an average length of five inches at maturity, and are capable of holding variable amounts of liquid, depending on the shape (Fig. 17). The central cavity is cylindrical and begins about 1 to 1 1/2" from the base, and reaches its largest diameter about the midpoint of 3/4 along the length of the leaf. The size of the cylinder then decreases to about half its maximum diameter near the mouth of the pitcher. The mouth consists of a rolled collar known as the nectar roll. A leaf flap continues upward and outward for another inch or more beyond the collar. A keel or ridge extends from the collar to the basal area on the uppermost side of the pitcher. The outer surface of the leaf has numerous glands and slender hairs which probably serve to direct prey toward the mouth.

Interiorly, the leaf is complex and can be divided into distinct zones according to structure and function. The upper zone (1) consists of a flap-like appendage (Fig. 18). It surrounds the mouth of the pitcher on three sides, forming a funnel. Its surface is covered with nectar glands and downward-directed hairs or spines. These serve to direct the prey's movement

toward the mouth of the pitcher. The next zone (2) has slick, downward pointing ridges and more nectar glands. Zone 3 is highly waxed (cutin) and very smooth. This surface offers no foothold and the prey fall into the fluid below. Zone 4 is usually considered the zone of absorption, and is not cutinized. It has numerous downward pointing hairs. Zone 5 is the lowest one. It is a very small zone devoid of hairs and its surface is relatively smooth. Its function is undetermined. The liquid held within the leaves is a dilute solution of proteolytic enzymes and rain water. It is believed that these enzymes are secreted from the upper zones of the leaf. The different zones of the leaf interior play an important role in the ecology of both *S. purpurea* and *W. smithii*. For a more detailed description of the zones and their function, the reader is referred to Plummer (1966a, b), Lloyd (1942), Macfarlane (1889, 1893), and Cooke (1882).

Flowers of *S. purpurea* are borne on long, slender, leafless stalks. They have reddish-purple sepals, conspicuous red petals, and an inverted, umbrella-shaped style. The style bear five ribs and the tips of these are the stigmas (Fig. 19, 20).

The seeds are light brown in color and measure 1 1/2 to 2 mm. long and 1 mm. wide. They are relatively flat with a keel along one side. One plant may yield several hundred seeds but few seeds produce viable plants. Seed dormancy is broken by periods of two to three months at 5°C (Mandossian, 1966).

The plant is anchored within the sphagnum by strong ascending rhizomes clothed in the reminants of dead and decaying leaves. The plant sends out thick fibrous roots which may reach as far down as 18" to the free water zone of the bog (Fig. 21). The roots, as in other carnivorous plants, are devoid of mycorrihiza.

Measurements of all the leaves of a small number of plants from the Pinawa and Kenora bogs were made (Table 2). The size of leaves (50%) varied between 11 to 30 ml. with a mean of 14 to 20 leaves per rosette.

(ii) Life Cycle of *S. purpurea*

Because of the close relationship of the life cycle of *W. smithii* to that of *S. purpurea*, it is necessary to fully understand the succession of events in the life cycle of the plant. At the beginning of the study (May 1969) overwintering leaves, produced the previous summer, were examined. They are characteristically mature in appearance, exhibiting a dark green or reddish-brown color. Dead flower stalks, often without any remnants of the flower or seed pod, can be found standing erect at the center of the encircling leaves. Most leaves are intact and still hold fluid; others show some evidence of decay (Fig. 22). The intact leaves retain a reasonably healthy appearance during May and June, and even into July, but decay is inevitable. By the end of July, virtually all of the overwintered pitchers rot away. Leaf decay begins at the tip. The flap turns brown and withers. As decay progresses downward, the leaf tissue becomes blackened and gummy, eventually breaking away and releasing the fluid held within the leaf. All that remains is the basal portion (Fig. 23, 24).

New leaves (1969) were first observed near the end of May and early June. These began as short green/reddish blades (Fig. 25), which grew rapidly throughout June and July. The first leaves opened during the early part of July and continued to open until early August. New leaves are easily distinguished from those of the previous year by their color and succulence. Old leaves are dark green with extensive reddish hue and venation; young leaves are soft, light to medium green in color and the venation is subdued (Fig. 26).

Table 2

Frequency percentage of leaf size and leaf number per rosette, June 1970

Leaf Size (in ml)	Pinawa %	Kenora %
0-10	9.5	9.8
11-20	35.7	41.5
21-30	35.7	22.0
31-40	19.0	14.6
41-50	-	4.9
>50	-	7.3
n =	42	41
Mean leaf size	22.67	24.85
Mean No./rosette	14.0	20.5
n =	3	2

Mean number of leaves/rosette at both sites = 16.6

Greater than 50% leaf size = 11-30 ml

Old leaves die and decay by the time the new leaves mature.

Flowers first appear as small red buds about the end of May or the beginning of June. The buds enlarge, and the stalks elongate rapidly, coming into full bloom during the middle of June through to August (Fig. 27, 28).

When first open, the pitcher leaves are either dry or contain no more than a few drops of fluid, possibly secreted by the plant. Later, the leaves are filled with dew and rain water. The amount of fluid in the pitchers varies with the local conditions of rainfall and evaporation. Since the plants are overgrown by sphagnum and herbacious overgrowth, the humidity of their immediate surroundings is probably very high and evaporation can be expected to be minimal. Plants which were full of water were experimentally covered to prevent additional rainwater from entering, yet allow evaporation to occur. These were still half-full after three weeks during the month of August, 1969. The level of fluid in the leaves was influenced by exposure to rainfall and evaporation. The pH of the fluid was similar to that of the surrounding bog water, remaining at 4.5 to 5.0 through the season.

The leaves, once open, enlarge to their full size and hold water throughout the season. From about the middle of September to the end of October, the leaves are subject to periods of freezing and thawing. These freezing periods begin as short intervals during the night or early morning. Soon pitchers remain frozen except for a few hours each day. Once they are covered with snow, about early November, they remain frozen until the snow melts (mid-April).

During October 1969, the leaves for the subsequent year had already started their growth. Later investigations revealed that this growth commences as early as the middle of August (Fig. 29), but the leaves become

dormant, that is, growth is probably inhibited by environmental conditions. Growth starts again in the spring as soon as climatic conditions are favorable. The flower bud appears to follow the same pattern and can be found in the fall by pulling apart the enshrouding leaves at the center (Fig. 30). Flower buds and leaves brought to the laboratory in December 1970, began to grow when left at room temperature and high humidity, some reaching almost full bloom in three weeks (mid-January). Therefore, the leaves examined in the spring of 1969 (overwintered leaves) actually began their growth in the fall of 1967, rather than in the spring of 1968. The bud and leaflets found in August 1970 will make their appearance in the early summer of 1971 and persist through to the summer of 1972.

As Judd (1959) had found, there is a period of 35 to 40 days in which the leaves of two generations are present (mid-June to mid-July) and in which populations of inquilines could exist in leaves of both years and allow a transfer of the populations from the old leaves to the leaves of the current year. Eggs and first instar larvae of *W. smithii* can be found in new leaves within two weeks after they open. Figure 31 summarizes the succession of events in this growth cycle.

(iii) The Habitat

The four bogs (Kenora, Telford, Pinawa, and The Pas, Figure 1) in which this study was carried out are typical of the many bogs which occur in the boreal forest areas in Manitoba and northern Ontario. Bogs in general begin with the covering and filling of shallow lakes in progressive stages, until the entire lake is covered. The succession ends in a climax spruce or deciduous forest. This succession is shown diagramatically in Figure 32 (after Smith, 1966).

The bog located southeast of Kenora exhibits the early stages of this succession (Fig. 33). Here, *S. purpurea* is found in the floating sphagnum mat where *Chamaedaphne calyculata* (leather leaf) and *Ledum groenlandicum* (labrador tea) begin and continues into the bordering *Picea mariana* (black spruce). A transect from the lake margin to the black spruce and beyond this to the birch and poplar stands gives an excellent perspective of the trend of succession as all stages show in Figure 32, are represented.

The Telford, Pinawa, and The Pas bogs are representative of stage E. The Telford bog appears to be the youngest of the three, as the predominant tree growth is *Larix laricina* (tamarack). The trees are sparce and small, seldom reaching fifteen feet. The Pinawa Bog is somewhat older, having both *L. laricina* and *P. mariana* (Fig. 34). The Pas bog is the oldest, in terms of plant succession at least, as the dominant trees are *P. mariana* (Fig. 35). In all three of these bogs, *S. purpurea* can be found grouped sporadically in clumps, and frequently only on sphagnum hummocks (Fig. 36). Factors determining the distribution of *S. purpurea* within the bog and the factors determining its absence in many bogs are not known.

A more detailed study of the bog in the Pinawa area was conducted in the fall of 1969. The Pinawa Bog is located in an area at the western edge of the Precambrian Shield, forming a transition zone between the Aspen parkland to the west and the coniferous forests to the east and north. Within the study area, a variety of vegetation can be found with species representative of both forest types. Specimens of *Populus tremuloides, Populus balsamifera, Betula papyrifera, Quercus Macrocarpa, Prunus pennsylvanica,* and *Prunus virginiana* can be found in the dryer areas. *Thuja occidentalis, Picea mariana, Larix laricina,* and *Salix* spp. dominate the wetter areas. Figure 37 is an aerial view of the FIG area in the Pinawa Bog and it was appropriately selected by AECL researchers, as representative of the Aspen and Coniferous

Forest transition.

Beginning at the west side, the entrance to the 1000 meter circle known as FIG and progressing east, the predominant species were *Betula popyrifera, Abies balsamea, Pinus banksiana, Populus tremuloides, Populus balsamifera* and *Picea glauca* (A), followed by a transition zone of mainly *Thuja occidentalis,* (B), then into the true bog area (C) of *Picea mariana* and *Larix laricina.* One hundred meter grid lines were cut, transecting the circle west to east and north to south. Studies of *W. smithii* were concentrated in grids one and two (Fig. 37). Grid three was used solely for determining plant species and their abundance (Table 3). The check list may not be definitive as the survey was made at only one time during the year (October). A check list was not attempted at the Telford, Kenora, or The Pas bogs, but in general the plants recorded from the Pinawa Bog were also observed in the other bogs.

(iv) Distribution of Plant Species

In an attempt to understand the spacial distribution of plant species within the Pinawa Bog, a study was carried out using a method developed by McGinnis (1934). This method makes use of the mathematical relationship between the frequency and density of the various species in a plant community. The main interest here was, of course, the distribution of *S. purpurea.* Using a table of precalculated expected densities for any given frequency percentage, it is possible to determine an expected density (d) for any known frequency. The expected density is then compared with that of the observed density (D) and the value obtained is an indication of the degree of aggregation. Generally, D/d values greater than 2.0 indicate that the species under consideration is aggregated. Values less than 1.0 indicate a tendency toward

Table 3

A check list of the plant species collected October, 1969 in the Pinawa bog.

Species	Common Name
Andromeda polifolia	Wild Rosemary
Betula glandulosa	Dwarf Birch
Carex spp.	Sedges
Chamaedaphne calyculata	Leather Leaf
Drosera rotundifolia	Sundew
Eriophorum angustifulium	Cotton Grass
Gaultheria procumbens	Checkerberry
Kalmia polifolia	Bog Laurel
Larix laricina	Tamarack
Ledum groenlandicum	Labrador Tea
Lycopodium spp.	Club Mosses
Maianthenum canadense	Lily-of-the Valley
Menyanthes trifoliata	Buck Bean
Picea mariana	Black Spruce
Sarracenia purpurea	Pitcher Plant
Sphagnum spp.	Sphagnum Moss
Vaccinium oxycoccus	Bog Cranberry

Table 4

Calculation sheet for spatial distribution samples in the Pinawa bog, October 1969

Species	No. of Quadrats	No. of Plants	Frequency %	Expected Density (d)	Observed Density (D) No. of plants/No. of Quadrats	D/d
Chamaedaphne calyculata	16	1383	16/20= 80%	1.61	69.15	42.95
Ledum groenlandicum	12	668	12/20= 60%	0.92	33.40	36.30
Kalmia polifolia	13	134	13/20= 65%	1.05	6.70	6.38
Vaccinium oxycoccus	20	7573	20/20= 100%	6.91	378.65	54.80
Betula glandulosa	9	84	9/20= 45%	0.60	4.20	7.00
Maianthenum canadense	16	1160	16/20= 80%	1.61	58.00	36.02
Eriophorum angustifolium	6	148	6/20= 30%	0.36	7.40	20.56
Larix laricina	7	8	7/20= 35%	0.43	0.40	0.93
Picea mariana	11	51	11/20= 55%	0.80	2.55	3.19
Sarracenia purpurea	14	85	14/20= 70%	1.20	6.71	5.59
Andromeda polifolia	15	437	15/20= 75%	1.39	21.85	15.72
Carex spp.	15	264	15/20= 75%	1.39	13.20	9.50

regularity in distribution. For the purposes of this study, the same criterion were used.

The quadrat size was one meter square, the recommended size for sampling herbaceous vegetation. A total of twenty quadrats were taken at random within the 100 meter grid. The species and total number were counted. Actual counts are given in Appendix C. Table 4 compiles the following: the number of quadrats in which the various species were found, the total number of each species found, frequency percentages, expected densities (d), observed density (D), and the D/d values. From this data the various species were graded as to their spacial distribution based on the previously stated criteria. Figure 38 shows graphically the degree of aggregation of the various species.

From the results it can be seen that only one species (*Larix laricina*) approaches the value which would indicate random distribution. All other species appear to be aggregated, *V. oxycoccus, Chamaedaphne, Ledum,* and *Maianthemum* showing the greatest degree of aggregation. *Carex, Betula, Kalmia Sarracenia,* and *Picea* tend toward randomness. *S. purpurea* and *L. laricina* show the greatest affinity toward randomness of distribution.

It was noticed that *S. purpurea* did not occur in some areas of the bog but did in others, with no apparent change in associated vegetation. It was not until later that differences in tree densities were noticed, with *S. purpurea* occuring in the areas of low tree density and not in areas of high tree density. In turn, low tree density can be visually correlated to drainage patterns in the bog. Figure 39 diagramatically shows the relationship of tree density to the drainage pattern in the Pinawa Bog. The drainage way also shows up on the airial photograph in Figure 37 as a lighter area running north-north east to south-south west. The three 100 x 100 m. grids sampled are in this area. These drainage ways are the wettest areas of the bog, and it is

possible that the excess moisture limits tree growth. It may be the moisture or the reduced competition for sunlight that favors the colonization of *S. purpurea* in these areas.

(v) Geographical Distribution of *S. purpurea*

In reviewing the literature, it became apparent that the presently published maps of the distribution of *S. purpurea* in North America were not satisfactory, particularly with respect to the distribution in Canada. Neither its western nor its northern limits were known and most publications referred to its range as being from "Florida to Labrador". Figure 40 records the sites from which *S. purpurea* have been collected in Canada. The more northern and western locations are also given a numerical code. The actual location and reference for each coded location is given in Appendix D. A new map (Fi.g 41) which shows the recorded distribution of *S. purpurea* in North America is also presented.

The distribution of *S. purpurea* may extend as far west as the British Columbia/Alberta border, having been reported from Edson and Hinton, Alberta. The northern distribution extends as far as Goose Bay and Indian Harbor, Labrador (54°30'N) in the east to Hart Lake, N.W.T. in the west. This latter site is, as yet, uncollected but since collections from Lake Athabasca (59°01'N) are known, it is likely that it does. Scoggan (1957) reports it from Great Bear Lake, N.W.T. Because present collections in these more remote regions are limited, the known range will probably be extended even further north with subsequent collections.

The precise manner in which *S. purpurea* became established in bogs and its migration northward is one of the most interesting studies in post-glacial distribution. Accepted theories suggest that: (1) *S. purpurea* was in

existence before the Pleistocene glaciations. With the onset of the glaciers, *S. purpurea* disappeared rapidly, possibly surviving in some refugium. At the end of the Ice Age, it reoccupied large areas in the wake of the retreating glaciers. (2) That the present-day form evolved during the glaciation on response to special glacial conditions from an ancestoral form. Thus, the present-day distribution is not preglacial, but postglacial (Croizat, 1952).

Some authors recognize two subspecies of *S. purpurea: S. purpurea venosa*, which is believed to be a relic of the ancestoral forma and is sparsely distributed along the coast of southeastern U.S.A. as far north as New Jersey; and *S. purpurea gibbosa*, which extends northward from New Jersey, ranging widely east, west, and north into Canada. It is this latter subspecies to which the previous two theories are applicable. Wherry (1935) maps the range of the two subspecies and discusses the possible migration northward. Whether or not two subspecies do exist is still a subject of controversy among plant taxonomists.

Postglacial records, based on pollen samples, have shown that *S. purpurea* was present in bogs 7,000 years ago (Terasmae, 1968). Because the pollen of this species is small, thin-walled, and delicate, it may not preserve well in bog desposits. In addition, *S. purpurea* is not a wind pollinated species and its pollen is not distributed over the bog surface.

(vi) Associated Fauna

Two insect species are found breeding only in the pitcher plant. These include *Metriocneumus knabi* Coquillet, a chironomid, and *W. smithii* (Coquillet). The bionomic of *M. knabi* is given by Weins (1971). Other arthropods use use the pitcher plant as either a primary and occasional habitat. Some that have been taken in routine collections are larvae of *Blaesoxipha fletcheri*

(Aldrich), *Endothenia daeckeana* Krt., *Exyra rolandiana* Grt., the water mite *Anoetus gibsoni* (Nesbitt), and aphid of the genus *Macrosiphum*.

The larva of *B. fletcheri* was collected from pitcher plants at each collecting site. The eggs are deposited in the pitchers and the larvae feed on the trapped insects. When full-grown they leave the pitcher and pupate in the sphagnum. Although more than one larva may begin development in each pitcher, it appears that only one per pitcher develops to maturity, the weaker one(s) having fallen victim to the carnivorous attitude and superior strength of the survivor. When more than one larva was placed in a small dish in the laboratory, they were cannibalistic, feeding upon one another whenever contact was made, with the larger usually surviving.

The larvae of *E. daeckeana* have been observed to feed on the flowers, and later the ovary of *S, purpurea*. At pupation, cocoons are spun among the refuse at the site of feeding. Infected seed pods tend to remain intact on the withering stem rather than releasing their seed and falling from the stem. In the fall of 1969 at The Pas site, 75% of the dried flowers and seed pods found remaining on their stems were infected with one or more of these larvae. Infected flowers degenerate, turn brown, and droop from the stem (Fig. 42). Seed pods bear a small hole where the larvae made their entrance. Debris (fecus) and silk is evident as well. The normal flower is shown in Figure 43 as a comparison.

Larvae of *E. rolandiana* hatch from eggs laid on the inner walls of the pitchers. The larvae eat a thread-like groove around the collar of the pitcher (Fig. 44). This causes the upper portion, the flap, to die and the collar curls inward, effectively sealing the pitcher (Fig. 45). The larvae then feed on the inner surface of the pitcher, reducing the walls to a paper-thin skeleton. The adults later escape through the wall of the pitcher. *E. rolandiana*

were observed only at the Pinawa Bog.

The water mite, *Anoetus gibsoni*, was collected from pitchers at all four study sites. At the Pinawa site, one adult female and two nymphs of *Macrosiphum* (possibly species Nova), Aphididae, were collected.

Chapter 5

PHOTOPERIODIC INDUCTION, MAINTENANCE, AND TERMINATION OF DIAPAUSE IN *W. smithii*

Photoperiod is known to be one of the major environmental factors controlling the seasonal cycles of many organisms (Beck 1968). Plants, vertebrates and invertebrates, are all affected by daily periods of light and dark, and the annual changes that occur in these periods. Daily cycles of light and dark provide a link between the organism and its environment, through which environmental information is communicated to the living system.

Several factors have been implicated in the control of diapause in insects but daylength has proved to be of greatest importance and has been the subject of many reviews [Andrewartha (1952), Hinton (1953, 1957), Lees (1955, 1956), Harvey (1962), de Wilde (1962), Beck (1963, 1968), and Danilevskii (1965)].

Photoperiodic control of larval diapause in *W. smithii* was first demonstrated by Jenner (1951), who showed that development was continuous when larvae were reared at periods of 15 hours, or more, of light per day, whereas development stopped in the third instar during periods of 13 1/2 hours of light per day or less. Until now, no studies had been carried out on the photoperiodic induction of diapause, critical photoperiodic ranges, nor of the stage(s) responsive to these photoperiodic stimuli in *W. smithii*.

A. Characteristics of Diapause Larvae

Diapause has been called a state of physiological rest (Danilevskii 1965), but it is not a completely inactive state. During diapause

physiological functions and changes continue, although at a reduced level, progressing in a definite direction, ultimately resulting in the capacity for active development.

Several general physiological features have been linked as responses to the diapause state in insects. Among these are lower metabolic levels, reduced or complete cessation of the feeding processes, low respiration rates, decrease in total body water, and the presence of abundant deposits of reserve food material. In addition, resistance to desiccation, cold-hardiness, supercooling, and the survival in spite of ice formation within the body tissues have been attributed to the phenomenon of diapause.

In *W. smithii*, three physiological aspects of diapause were examined: respiration rates, feeding rates, and cold tolerance. Cold tolerance of *W. smithii* is discussed separately in Chapter 6.

(i) Respiration

Diapausing third instar larvae of *W. smithii* are visually indistinguishable from non-diapausing larvae and separation of field populations is impossible without waiting several weeks to see which will continue development and which will remain in the third instar stage. The larvae of both types are equally active when held under the same conditions. To determine the differences, if any, that exist in their respiration rates (which would also give an indication of differences in metabolic processes) trials were conducted on the various groups using a Gilson Differential Respirometer (Chapter 3).

Several groups of larvae were compared on the basis of respiration rates (measured as microliters/larvae/hour), including diapausing and non-diapausing third instar (both field-collected and laboratory-reared material), fourth instar, and second instar larvae. The main interest,

however, was the comparison between the diapausing and non-diapausing groups. The respiration rates of the various groups are presented in Table 5. The respiration rates of fourth instar larvae (at 25°C) were higher (1 1/2 times) than those of third instar larvae (either diapausing or non-diapausing). Respiration rates of second instar larvae did not differ significantly from those of third instar larvae. While differences were expected in the rates between diapausing and non-diapausing third instar, no significant differences were detectable.* A strong correlation was shown, however, between treatment and storage time and it is possible that holding diapausing third instar larvae may affect the respiration rate and obscure the true rates.

(ii) Feeding rates

Smith (1901) noted that *W. smithii* larvae upon release from the ice engaged in apparent feeding. However, observations of laboratory cultures suggested that diapausing larvae, although appearing to feed, consumed considerably less food than non-diapausing larvae. Investigations were carried out to determine what differences might exist in feeding rates of diapausing and non-diapausing third instar larvae.

Visual comparisons were carried out first, using the method described in Chapter 3. The rates of ingestion of three groups of larvae were compared: (1) non-diapausing third instar reared in the laboratory at 18L:6D and 27°C; (2) diapausing third instar reared in the laboratory at 12L:12D and 20°C; and (3) diapausing third instar larvae collected from the field (collected January 29, 1971) and held at 12L:12D and 20°C. Advancement of ingested particles was classified as A (up to 1/2 full), B (1/2 to 3/4 full), and C (3/4 to full) (Fig. 46). Rate of ingestion was calculated as the percent

*Results compared using two-way analysis of variance with unequal subsamples.

Table 5

Average Respiration Rates (microliters/larva /hour) for Five Different Larval Groups.

Trial	Temperature	Duration of Test (Hours)	Diapause 3rd Instar	Non-Diapause 3rd Instar		4th Instar		2nd Instar
			Field Coll.	Field Coll.	Lab. Reared	Field	Lab.	Lab.
1	20°C	12	.103	.116	.200	-	-	-
2	25°C	7	.190	.248	.443	-	-	-
3	25°C	9	.210	.234	.172	.543	.551	.203
4	25°C	10	.168	-	.234	-	-	-
5	25°C	7	.223	-	.232	-	-	-
6	25°C	12	.221	-	.271	-	-	-

in each classification. Prior to treatment the larvae had been starved for 48 hours. Treatment involved placing the larvae in a distilled water and ink media for a period up to 25 days (Fig. 48). From the results, it can be seen that both the non-diapausing and diapausing third instar larvae reared in the laboratory had similar ingestion rates and all were completely glutted after two days in the China Ink media. Field-collected diapausing third instar larvae fed very little, and at the end of 25 days, few (11%) had reached stage C; 69% still had not fed at all. The fact that laboratory-reared diapausing larvae feed rapidly and field-reared diapausing larvae do not, may be explained, in part, by the fact that the field collection was made on January 29, after larvae had been in diapause for six months and in the frozen pitcher fluid for three months. Those reared in the laboratory had not been in diapause for more than one month. These larvae were still feeding actively, possibly to build up food reserves.

A second trial was carried out to see if ingestion rates would differ if larvae were fed a nutritive diet (standard larval diet), rather than a China Ink diet. Larvae were first fed (to gut stage B or C) on China Ink for four days, then placed in distilled water with standard larval diet. These were then checked after 3, 6, 9, 12, and 24 hours and the replacement of the carbon particles with normal diet was noted (Fig. 47). Figure 49 shows the percentage of larvae in each gut stage at the various time periods. The three stages were D (up to 1/2 replacement), E (1/2 to 3/4 replacement), and F (3/4 to full replacement) (Fig. 46). Again there was little difference between the non-diapausing and laboratory-reared diapausing larvae. The field-collected larvae still showed a slower rate than the other two groups, but the rate was much higher than that shown in the previous test. This may be due to the fact that these larvae had been stored at 12L:12D and 20°C for

about one month prior to the test, whereas the previous field-collected larvae were tested within a week of collection.

Feeding rates were also compared using radiocesium (^{137}Cs) labeled dog food. Larvae were allowed to feed on the labeled dog food for 1, 3, 6, 12, and 24 hours, after a starvation period of 48 hours. The photoperiod regime was 18L:6D and the temperature 27°C. The uptake (ingestion rate) was measured in counts per minute on a low level beta counter. The results are plotted graphically in Figure 50. The mean ± standard deviation counts are given in Appendix E, Table 1. From the results, it can be seen that significant differences are detectable within one hour after the beginning of the experiment and that while non-diapausing larvae showed rapid increases in counts/minute, diapausing larvae showed no increase at all.

Since mosquito larvae are known to regulate their ionic balance through ion-permiable regions of the body wall (see Clemments, 1963), a preliminary experiment was carried out to see if differences could be noted in diapausing and non-diapausing third instar larvae reared in nutrient-free media containing only ^{137}Cs solution and samples were taken and counted after 3, 6, 12, 24, and 48 hours. The results are given in Appendix E, Table 2, and shown in Figure 51. A comparison of the means revealed that a significant difference (P .05) existed between the two groups up to six hours after treatment was begun. However, at 12, 24, and 48 hours, no significant differences existed. The rate of increase in counts/minute for the diapausing group increased at a steady rate while the non-diapausing group increased rapidly up to 12 hours, then tapered off.

B. Induction of Diapause

Preliminary experiments indicated that larvae reared from eggs at

18L:6D and 25°C would complete development in 25 to 30 days. Larvae reared at 12L:12D and 25°C would develop normally to third instar, but would progress no further until placed at longer photoperiods (18L:6D). Third instar larvae, when transferred from 18L:6D to 12L:12D at 25°C continued development uninterrupted. These early experiments suggested that (1) the critical photoperiodic range was between 12 and 18 hours; (2) a stage prior to the third instar was the stage receptive to shorter photoperiods and thus responsible for the expression of diapause in the third instar stage.

In order to determine both the critical photoperiod and the receptive stage(s), first, second, and third instar larvae were reared at various photoperiods at 25°C and the percentage molting to fourth instar noted. The methods are outlined in Chapter 3. The stage(s) preceeding the test stage were pre-conditioned at 18L:6D and 27°C. The results after 5, 10, 20, 30, and 40 days at the various photoperiods and for the three different test groups are shown in Table 6. The percentage molting to fourth instar after 40 days at the various photoperiods and for the three different groups are shown in Figure 52. The critical photoperiod range was between 14 1/2 hours to 16 1/2 hours, the incidence of diapause decreasing with increasing photoperiod. At 16 1/2 hours light, or more, larval development proceeded uninterrupted, regardless of the stage at which it started. At 14 1/2 hours light, or less, only 5 to 10% of those larvae started at first instar progressed beyond the third instar stage; of those started as second instar, 35 to 67% progressed beyond the third instar when reared at photoperiods of 14 1/2 hours or less; those begun as third instar progressed uninterrupted regardless of the photoperiod.

Apparently first instar larvae and some second instar larvae (possibly young seconds) are responsible for monitoring the photoperiodic cues leading

Table 6

Percentage of larvae molting to 4th instar when reared at various experimental daily photoperiods at 25°C. Preconditioning consisted of rearing larvae to various stages at 18L:6D/27°C

Stage(s) Preconditioned at 18L:6D/27°C	Daily Experiment Photoperiod	Larval Stage at Start	Per cent of survivors progressing to 4th instar					
			5 days	10 days	20 days	30 days	40 days	n
E		1	0	0	0	0	0	30
E,1	10L:14D	2	0	35	27	35	35	30
E,1,2		3	12	93	96	96	100	30
E		1	0	3	7	7	7	120
E,1	12L:12D	2	0	36	45	48	49	120
E,1,2		3	30	85	94	97	97	120
E		1	0	8	8	9	10	60
E,1	14L:14D	2	2	46	47	50	52	60
E,1,2		3	46	95	97	97	97	45
E		1	0	6	4	5	5	120
E,1	14½L:9½D	2	15	63	69	67	67	40
E,1,2		3	75	93	100	-	-	40

E - Egg 1 - 1st instar 2 - 2nd instar 3 - 3rd instar

Table 6 (continued)

Stage(s) Preconditioned at 18L:6D/27°C	Daily Experiment Photoperiod	Larval Stage at Start	Per cent of survivors progressing to 4th instar					
			5 days	10 days	20 days	30 days	40 days	n
E		1	0	2	8	10	10	70
E,1	15L:9D	2	6	40	45	45	55	70
E,1,2		3	89	98	98	98	98	55
E		1	0	4	32	15	15	80
E,1	15½L:8½D	2	4	32	57	57	57	80
E,1,2		3	59	87	96	98	100	80
E		1	0	8	29	37	43	140
E,1	16L:8D	2	4	43	62	73	78	140
E,1,2		3	55	90	47	97	97	125
E		1	0	18	65	70	100	80
E,1	16½L:7½D	2	6	52	81	88	100	80
E,1,2		3	44	76	97	100	100	80

Table 6 (continued)

Stage(s) Preconditioned at 18L:6D/27°C	Daily Experiment Photoperiod	Larval Stage at Start	Per cent of survivors progressing to 4th instar 5 days	10 days	20 days	30 days	40 days	n
E		1	0	11	93	100	100	70
E,1	17L:7D	2	0	71	97	98	100	71
E,1,2		3	50	83	100	100	100	55
E		1	0	40	96	100	-	65
E,1	18L:6D	2	0	77	95	100	-	60
E,1,2		3	32	97	100	100	-	45

to the expression of diapause in the third instar.

Larval diapause in *W. smithii* is determined by the photoperiod to which the larval stages have been exposed. Diapause in these experiments was noted as a failure to molt to the fourth instar larval stage after a reasonable period of time (40days) at 25°C. *W. smithii* exhibits what Beck (1968) refers to as "Type I" induction curve ("long-day response") in which relatively long daylengths tend to favour continuous growth, while short days favour diapause.

C. Maintenance of Diapause

Once diapause is induced, third instar larvae can be held at short daylengths (14 hours or less) for several months, particularly if the temperature is lowered. For laboratory cultures, diapausing larvae were maintained at 12L:12D and 20°C with only a small percentage (5%) molting to fourth instar larvae after two months, after which mortality rises sharply. When larvae were held at 12L:12D at 10°C, the holding time could be doubled (four months) provided the water was changed periodically to prevent fouling.

D. Termination of Diapause

Diapause in larval Diptera which is induced by short-day photoperiods can generally be terminated by a long-day photoperiod (Beck 1968). Termination of diapause in third instar larvae of *W. smithii* was noted when the larvae molted to fourth instar, under long daylengths. Field-collected larvae, collected after the onset of diapause under natural conditions, were held at 12L:12D and 20°C for four weeks to ensure that the larvae were in diapause. The larvae were then placed at various photoperiods at 20°C and the percentage molting to fourth instar after 30 days was noted. The percentage molting to fourth instars after 5, 10, 20, and 30 days at each photo-

period is shown in Table 7. The percentage after 30 days is shown graphically in Figure 53. The proportion of larvae breaking diapause increased with increasing length of day, reaching 100% at a photoperiod of 16L:6D. Response of diapausing larvae of *W. smithii* to long-day photoperiods was rapid, larvae molting to fourth instar soon (within five days) after transfer to the non-inductive regime. No differences were noted in termination responses between larvae used immediately upon collection from the field, after being stored for one month, or between those which had been overwintering in the field for several months as was also noted by Smith and Brust (1971). A photoperiod of 0L:24D was as effective in terminating diapause as were long-day periods. *A. atropalpus* responds in a similar manner (Anderson 1968). These results suggest that overwintering *W. smithii* larvae are capable of progressing to fourth instar at any time, even before the onset of winter, and require only favourable photoperiods for development. Since growth in the field does not begin as soon as the critical photoperiod is exceeded (before May 1), factors other than photoperiod must act to prevent growth in the early spring.

E. Temperature Growth Threshold

Whereas photoperiod limits development in the fall, temperature appears to limit development in the spring. To determine the temperature threshold in *W. smithii*, three groups of larvae were reared at five different temperatures (27°, 20°, 15°, 10°, and 5°C) at a long-day (non-diapausing) photoperiod (18L:6D). The percentage molting to fourth instar at the various temperatures for each of the three test groups (laboratory-reared diapausing third instars; field-collected diapausing third instars; and laboratory-reared non-diapausing third instars) over a period of 50 days was noted, the results being shown graphically in Figure 54. The results show that in

Table 7

Percentage of 3rd instar larvae molting to 4th instar when placed at various photoperiods at 20°C. Prior to trials larvae were reared (or held in the case of field collected larvae) to 3rd instar at 12L:12D/20°C

Daily Photo-Period	n (3rd instar)	% of survivors molting to 4th instar			
		5 days	10 days	20 days	30 days
0L:24D	120	0	0	44.8	89.7
4L:20D	40	0	0	0	0
8L:16D	120	0	0	4.5	5.4
12L:12D	141	0	2.8	3.6	4.3
14L:10D	40	0	0	0	3.7
14½L:9½D	105	0	0	1.9	7.8
15L:9D	166	0	6.8	24.2	31.6
15½L:8½D	115	0.9	6.5	20.0	25.5
16L:8D	155	0.7	16.8	67.4	83.9
16½L:7½D	100	1.1	34.9	87.5	88.9
17L:7D	80	0	71.0	96.3	95.2
18L:6D	40	2.5	8.1	95.2	94.4
20L:4D	40	0	0	82.6	100.0
24L:0D	120	0	33.3	79.3	100.0

both field-collected and laboratory-reared diapausing larvae, growth is inhibited at a temperature of 15°C and lower. In the case of non-diapausing larvae growth did occur (very limited) at 15°C, but not at 10° or 5°C.

F. Natural Photoperiods

In the field, *W. smithii* experiences a variety of photoperiods, ranging from 8 hours to a maximum of 16 1/2 hours light at Pinawa (50°15'N-95°50'W). The daylength cycle is shown in Figure 55, and corresponds to the period during which other meteorological data was recorded. Setting 14 1/2 hours as the critical photoperiod, diapause is terminated about the middle of April and induced about the middle of August. In spring, however, growth is inhibited for about a month, until the temperatures (mean daily) rise above 15°C (see Fig. 60).

Chapter 6

COLD TOLERANCE IN *W. smithii* LARVAE

Insects which overwinter in the temperate zone are usually able to withstand moderately low temperatures for long periods of time. The only mortality directly attributable to temperature is from freezing whereas those insects that survive are free of any chilling injury (Salt 1961).

W. smithii is known to overwinter as a third instar larvae in the ice cores within the pitcher plant, *Sarracenia purpurea*. However, other than the preliminary investigations by Owen (1937) and Smith and Brust (1971, in press), the ability of *W. smithii* larvae to survive at low temperatures (particularly sub-zero temperatures) has been largely ignored.

(i) Survival at Sub-Zero and Low Temperatures

Observations of field populations during 1968-69 and 1970-71 indicated that the greatest mortality occurred during winter, with possibly 50% of the population being killed by the sub-zero temperatures (see Chapter 7). To assess the survival of *W. smithii* larvae at sub-zero temperatures, field-collected diapausing larvae were subjected to various low and sub-zero temperatures. Both groups were tested with and without pre-conditioning and the survival measured at various intervals after the test was begun (see Methods, Chapter 3). Comparisons were also made of diapausing and non-diapausing groups, and pre-conditioned and non-conditioned groups.

The percent survival of both conditioned and pre-conditioned diapausing larvae, and non-diapausing larvae at the various temperatures are shown graphically in Figures 56, 57, and 58. Third instar larvae did not survive

for more than three weeks at temperatures below -10°C. Constant temperatures of -5°C resulted in considerable mortality (60% in pre-conditioned larvae after 8 weeks; 70 to 90% in non-conditioned larvae after 8 to 10 weeks). Even a temperature of -1°C caused significant mortality (35% in pre-conditioned larvae after 8 weeks; 80% in non-conditioned larvae after 8 to 10 weeks). Pre-conditioning of the larvae aided in their survival, but did not lower the temperature at which they can survive. In non-diapausing third instar larvae, mortality reached 100% within 2 to 3 days at temperatures below -1°C. It is apparent that *W. smithii* possesses no particular ability to survive sub-zero temperatures, except for relatively short periods.

(iii) Supercooling of Larvae

Attempts were made to determine the temperatures larvae could withstand before freezing of the tissue occurred. Six different larval groups were tested. These were the following:

1. Diapausing third instar held at 12L:12D and 20°C for 3 months prior to the trials. (D3)

2. Diapausing third instar collected directly from the field (29/12/70). (D3F)

3. Diapausing third instar held at 12L:12D and 20°C for 1 month; 10°C for 2 months; 5°C for 1 month. (D3H)

4. Non-diapausing third instar reared at 18L:6D and 27°C. (ND3)

5. Second instar reared at 18L:6D and 27°C. (II)

6. Fourth instar reared at 18L:6D and 27°C. (IV)

The results are shown in Figure 59, which gives the mean±standard deviation and frequency percent at 0° to -5°, -5° to -10°, -10° to -15°, and -15° to 20°C for each test group. The individual supercooling temperatures are given in Appendix F. Although individual larvae supercooled (or froze) over a wide

range of temperatures (0°C to as low as -16.0°C), most did not survive temperatures below -5°C. A comparison of the means showed no significant differences in supercooling temperatures between the six test groups, although laboratory-reared second instar larvae supercooled to lower temperatures than that of other groups. None of the larvae recovered once they were frozen.

(iii) Snow Cover and Survival

Since *W. smithii* does not possess any particular ability to supercool or survive sub-zero temperature for long periods, snow cover must be instrumental in aiding winter survival of the larvae at this latitude. Daily temperature records were kept at Pinawa from October 1, 1969 to October 18, 1970, which indicated that the larvae did not experience temperatures much below -6°C (five day average), although air temperatures approached -32.0°C (five day average). The differences in temperatures were attributed to the insulating effect of the snow cover present. Figure 60 gives the five day mean temperature for both air and sphagnum (at the level where larvae occur) for 1969 to 1970 and clearly shows that the snow cover prevents extremes of temperatures. Snow depths for 1969 to 1970 are given in Figure 61. Although no correlation was attempted between snow depth and temperature, increased snow depth probably maintains the mild sphagnum temperatures as the air temperatures reach their minimum during January and February. Daily records are given in Appendix A. In addition to preventing extremes in temperatures, snow cover maintains a uniform temperature. During the period of snow cover, the larvae experience only small deviations in mean temperatures (Fig. 62). During winter collection (1970 to 1971) (29/XII/70 and 29/I/71) it was noted that the sphagnum was frozen only to about 15" below the surface and that free water could be found below this.

Chapter 7

THE BIONOMICS OF *Wyeomyia smithii* (COQUILLETT)

Studies of mosquitoes have been concentrated on those species of medico-veterinary importance and consequently, innocuous species such as *W. smithii* have received comparatively little attention. Several aspects of its bionomics are presented here.

A. Egg

(i) Description

The chestnut-brown egg of *W. smithii* can be found within the new leaves of the pitcher plant from about the end of June/early July through to the end of September. A detailed description of the egg is given by Barr and Barr (1969). When first laid, the egg is translucent, but soon darkens. The mean size is 444±23μ in length by 162±6μ in width. As Price (1959) found, fertile eggs can be readily distinguished from infertile eggs. In the former, the embryonic features are distinguishable after about 48 hours, and can be viewed through the chorion. The eyes, egg burster, and some larval hairs of the developing embryo can be seen (Fig. 63). The anterior end of the larva is located at the larger end of the egg and the dorsal surface of the larva lies along the convexed side. The head occupies the antior one-third of the egg with the thorax and abdomen contained in the remaining two-thirds. The chorion, itself, exhibits fine chronic detail when viewed microscopically using reflected light. The incubation period in the field and laboratory is 2 to 5 days with the majority of eggs hatching after 3 days.

(ii) Site of oviposition

Newly-opened leaves are preferred to the older (overwintered) leaves as sites of oviposition. Table 8 shows a comparison between a random sample of these two groups (July 23, 1969) at the Pinawa Bog, and shows the number of eggs and young larvae (first, second, and third instar) collected. Overwintered larvae have molted to fourth instar, pupae, or adults by this time, so first, second and third instar larvae found within the leaves must have been derived from eggs laid in the current year. The preference ratio for young leaves is approximately 4:1 (Table 8). This ratio is season-dependent, for later in the season only the current year's leaves are used.

Eggs are laid in leaves which have been open less than 24 hours (Fig. 64). The leaves open gradually to form a pitcher, and develop into a round-mouth container in about 48 hours. Once the opening is large enough to permit the entry of an adult female, eggs may be laid. Whether or not eggs are laid in "dry" pitchers as noted by Smith (1902), but refuted by others (Barr and Barr, 1969; Wallis and Frempong-Boadu, 1967) is possibly a matter of interpretation of the term "dry". Newly opened pitchers with eggs often contained no more than one or two drops of fluid at the very base of the pitcher cavity. In all likelihood, this was fluid secreted by the plant. The eggs were not in the fluid at the time of sampling, as the fluid was in the narrow base where females could not get to it. The eggs were commonly found higher up in the leaf cavity (zone 4) (Fig. 65, 66), where the relative humidity is undoubtably high even if no free water is present. The eggs would then be washed down into the lower portions of the leaf by rain. In older leaves (those that have been open for several days and have accumulated water) it is not possible to determine which eggs were laid on

Table 8

A comparison of numbers of eggs and larvae found in two random samples of pitcher leaves, (July 23, 1970), Pinawa, Manitoba. A - leaves that overwintered, B - current year's growth.

A				B			
Leaf Size (ml)	Larvae	Eggs	Total	Leaf Size (ml)	Larvae	Eggs	Total
42	14	3	17	30	16	2	18
49	9	6	15	34	61	13	74
42	7	2	9	40	19	3	22
32	3	1	4	37	-	77	77
36	3	1	4	37	6	-	6
31	-	3	3	24	11	5	16
40	10	-	10	30	6	-	6
41	3	-	3	38	21	-	21
35	8	-	8	30	11	5	16
38	10	-	10	25	29	2	31
43	5	-	5	28	33	6	39
52	1	-	1	35	55	19	74
30	5	-	5	21	7	-	7
33	1	-	1	40	-	17	17
38	3	-	3	42	21	12	33
31	14	-	14	33	-	38	38
45	3	-	3	25	-	24	24
33	10	-	10	19	4	4	8
Mean per leaf			6.94±4.89				29.28±23.36

the water and which were laid on the walls of the pitcher (Fig. 67).

(iii) Desiccation of eggs

Attempts to locate eggs in pitchers in the field often resulted in damage to the plant. Attempts to wash the eggs free of the leaves also proved impracticable as the eggs became lodged in the downward pointing spines (see Fig. 66). This may have some survival value if the leaf is accidently bumped or knocked over by a passing animal. As the fluid level in the leaves increases, eggs are often held firmly in place, remaining submerged rather than rising to the surface. Should the pitcher overflow, eggs would not be washed out. When the water level drops, the spines allow the eggs to follow the descent of the fluid, rather than becoming stranded and subject to possible desiccation. The spines or hairs do not hinder the movement of the eggs downward within the pitcher. Should hatching occur before the fluid level has risen to where the eggs are, the emerging larva move downward rather than upward due to the downward direction of the spines. Because of the high humidity within the plant, it is unlikely that the eggs of *W. smithii* are subject to any serious desiccation in the field, unless stranded in the upper portion of the pitchers. In the laboratory, almost total mortality occurs in eggs which have been desiccated for 24 hours.

(iv) Egg population in leaves

The number of eggs per pitcher leaf varied from 0 to as many as 100 or more (156 were taken from one leaf) (Table 9). The mean number of eggs per leaf at any particular date is misleading, as egg laying is not regular through the season and locality.

(v) Hatchability

By counting the number of larvae and viable eggs (those that hatched

Table 9

Variation in mean numbers per leaf (calculated as number of eggs plus larvae) in new leaves on various dates in 1969-1970 at Pinawa, Kenora and Telford

Location	Date	No. of Leaves Sampled	Eggs + Larvae	Mean No. Individuals per Leaf	Mean Leaf Size (ml)
Pinawa	23/7/69	8	180	22.5±26.8	-
	29/7/69	14	257	18.3±23.3	14.7±10.1
	5/8/69	10	167	16.7±14.8	21.6±10.5
	14/8/69	5	82	16.4±9.74	17.0±4.1
	23/8/69	7	227	32.4±28.7	27.9±11.8
	Overall Mean			20.8±21.9	
	3/7/70	16		4.4±5.5	17.9±5.6
	9/7/70	17		18.1±14.7	39.0±16.0
	18/7/70	19		42.1±21.0	33.8±11.2
	23/7/70	18		29.3±23.4	31.6±6.9
	29/7/70	21		26.0±16.3	27.6±6.1
	7/8/70	32		25.1±20.8	35.8±11.6
	13/8/70	38		20.3±14.9	31.8±9.5
	20/8/70	33		22.9±20.4	31.2±12.6
	27/8/70	37		26.1±22.6	32.3±12.8
	Overall Mean			24.0±20.2	

Table 9 (continued)

Location	Date	No. of Leaves Sampled	Eggs + Larvae	Mean No. Individuals per Leaf	Mean Leaf Size (ml)
Kenora	17/7/69	9	89	13.67±12.11	-
	23/7/69	9	103	11.44±9.5	-
	30/7/69	11	490	44.55±40.71	30.27±12.37
	13/8/69	7	120	17.14±17.10	27.43±13.06
	22/8/69	12	316	26.33±18.55	27.83±11.98
	29/8/69	7	325	46.43±40.60	24.71±19.22
	Overall Mean			21.21±27.29	
	5/7/70	16	35	2.19±2.56	
Telford	17/7/69	11	79	4.73±3.74	-
	21/7/69	10	65	6.5±7.92	14.6±9.14
	22/7/69	9	73	8.22±5.54	-
	29/7/69	9	173	19.22±7.95	18.89±5.67
	6/8/69	7	76	10.86±10.64	21.86±3.98
	14/8/69	6	34	5.67±2.25	19.0±4.94
	23/8/69	8	143	17.88±13.67	18.00±8.55
	27/8/69	7	96	13.0±10.94	11.71±2.14
	Overall Mean			11.28±9.73	
	8/7/70	9	132	14.67±13.17	17.56±7.92
	29/7/70	11	194	15.18±10.68	17.45±7.85
	11/8/70	10	253	25.30±30.66	22.90±11.79
	21/7/70	10	65	6.5±7.9	
	Overall Mean			15.19±18.42	

in the laboratory after 10 days), an egg viability of 87% was recorded throughout the summer at the Pinawa site. On some dates the hatchability was low, only 60 to 65%, while on other dates 96 to 98% of the eggs hatched. The hatchability of eggs on various dates at Pinawa are shown in Table 10.

B. Larva

The larva of *W. smithii* was described by Dyar (1901). The larvae found in the four study areas did not differ from the description by Dyar (1901) or the description given in Carpenter and LaCasse (1955).

Small and translucent by comparison to other mosquito larvae, the most striking feature that separates *W. smithii* larvae from those of other species, is the presence of only two anal papillae instead of the usual four. These are large and inflated, almost balloon-like, very transparent, and highly tracheated.

(i) Respiration

Since young larvae rarely come to the surface as early instars, respiration must be largely cutaneous. Most other species of mosquito larvae are surface breathers. *W. smithii* larvae can remain submerged for many hours or days. In the laboratory, third instar larvae survived under a film of oil for a period of eight days without any significant mortality. The possible function of the large tracheated anal papillae (gills) is one of respiration. Larvae can often be seen to lie on their dorsal side with the mouth (labral) brushes in constant motion. This creates water currents which pass dissolved oxygen over the anal papillae. However, there is at present no evidence in the literature to support this.

Oxygen concentration of the medium may also dictate which method of respiration is used by the larvae. Temperature, surface area, fungus and

Table 10

Hatchability of eggs in a field population, Pinawa, 1970. Eggs recovered from the leaves on each sampling date were kept in distilled water and the number of larvae recorded after 10 days.

Sampling Date	No. of Larvae Collected	No. of eggs			% Eggs Hatching
		Collected	Hatched After 10 days	Eggs + Larvae	(Eggs plus larvae) in plant leaves
July 3	0	70	54	70	78.6
9	53	252	168	305	72.5
18	212	590	264	802	58.3
23	270	227	102	497	74.9
Aug. 13	772	49	13	811	96.8
20	555	153	47	708	85.0
Sept. 16*	1130	82	2	1212	93.4
24	869	39	2	908	95.9
Oct. 1	596	10	-	606	98.3

* No adults seen after this date - first ice found in the pitchers.

N.B. This table does not take into account larval mortality. Although mortality probably occurs, no data is available. Percent hatch is calculated on the assumption of 0 mortality.

bacteria may all play a role in establishing the oxygen tension. Higher temperatures, and consequently lower dissolved oxygen levels, may be one reason why fourth instar (during June and July) give up their bottom activity and spend the majority of their time at the surface where direct contact is made with the air. At high temperatures, early instars also spend more time at the surface. Larvae of all instars will rise to the surface and remain there when the medium becomes eutrophic.

(ii) Feeding

Two methods of feeding are exhibited by the larvae of *W. smithii*: filter-feeding and browsing. Filter-feeding is typical of many mosquito larvae. These particles are sufficiently small enough to be ingested and passed directly to the digestive tract without further mastication. Filter-feeders are characterized by long thread-like, unserrated labral brushes, large maxillae, and weakly scelerotized mandibles (Goma, 1966; Pucat, 1965). Both "eddy" and "interfacial" filter-feeding is exhibited in *W. smithii* (Bates, 1949; Clements, 1963). Eddy type filter-feeding is carried out when the larvae are in the inverted position on the bottom. Rapid movements of the mouth brushes (Fig. 68) produce strong, eddy currents in front of the larvae. The current is directed toward the mouth and the particles are collected and combed out by the maxillary brushes, then swallowed. Interfacial feeding, which is done at the surface, is infrequent in *W. smithii* and has only been observed in laboratory cultures. There are no eddy currents created during interfacial filter-feeding; the particles of food floating on the surface are drawn in straight lines from all directions, being drawn first by the mouth brushes, then by the maxillary brushes.

Browsing involves the mastication of solid material into smaller particles which can be ingested. Browsers have shorter mouth-brushes (labral) than

filter-feeders, and the middle ones are at least serrated distally (Goma, 1966). Examination of the labral brushes of the larvae of *W. smithii* show that not only do the larvae behaviorally exhibit both types of feeding, but that the larvae are also structurally equipped for both types of feeding. Figure 69 shows that both serrated and unserrated thread-like labral brushes are present. The mandibles are not highly scelerotized and indicate that much of the food or particles ingested do not require further breakdown. There is no behavioral or structural indications of predatory habits.

(iii) Diet

The main diet of *W. smithii* larvae appears to be the decomposed remains of the trapped insects, and the microbiotic fauna and flora within the fluid of the leaves. Dissolved nutrients may play a role in the nutrition of the larvae. It is possible that the anal papilli play a role in the uptake and balance of inorganic as well as organic salts. The decomposing bodies of the trapped insects supply sufficient nutrients for the development of well nourished larvae and adults. The addition of artificial diets to pitchers in the field polluted the fluid and produced high mortality. Overfeeding of laboratory cultures also led to fouling and the development of fungal growth on both the uningested food and on the larvae.

The principle storage organ for food reserves is the fat body; a parietal sheet of cells applied to the epidermis throughout the abdomen and thorax (Clements, 1963). Well fed larvae of *W. smithii* contain large amounts of fat globules and are plump and quite translucent. Starved larvae appear thin and somewhat transparent. Diapausing third instar larvae appear to contain considerably more fat reserve than non-diapausing larvae. There is also an increase in fat body in late instar larvae (fourth), and much of the fat is carried over to the adult stage. Most adults have an abundance

of fat when they emerge, but this is rapidly depleted as ovarian development progresses.

(iv) Mobility

W. smithii larvae are capable of three types of movement. Most commonly used when alarmed is a swimming motion, comprised of a lashing motion of the whole body, moving the larvae tail first through the medium. This type of movement is utilized in both horizontal and vertical displacement. A second type is also common and is known as gliding. In *W. smithii* this method is commonly employed by undisturbed larvae and is often associated with feeding. The larvae propel themselves head first, in a horizontal plane, by the movement of the mouth brushes only. A third method exhibited is not observed in other species. This is a curling method in which the larvae twist their head and tail together in a ring-like fashion. This method is often used to allow the larvae to sink to the bottom rapidly. On rare occasions, larvae can be observed to take hold of small air bubbles in this ring-like manner and rise to the surface (see also Smith, 1904).

The larvae of *W. smithii* are most active during the first three instars, and most of this period is spent below the surface of the fluid. During the fourth instar, particularly as late fourth, the larvae spend much time at the surface and the most commonly observed movement is swimming.

Whereas low temperature (<15°C) inhibit growth, such conditions do not appear to restrict movement. Overwintering larvae, when thawed from the ice cores, can be seen to move even before all the ice has melted. Diapausing third instar larvae exhibit more activity at 5° to 10°C than do non-diapausing third instars, or second or fourth instar larvae.

W. smithii larvae are negatively phototactic, orientating to the darker areas of the rearing pans or to the recesses of the pitcher leaves. Larvae

at the surface, when disturbed, retreat rapidly to the darker portions of the container.

(v) Differentiation of instars

W. smithii, like all other mosquitoes, goes through four larval molts, or ecdyses. The thorax and abdomen, which are covered in a thin extensible cuticle, grow continuously throughout the larval period, but the head capsule and respiratory siphon, which are heavily scelerotized, do not. Both the siphon and head capsule grow immediately after ecdyses until the cuticle hardens. Measurements of head capsule grow immediately after ecdyses until the cuticle hardens. Measurements of head capsule widths in mosquitoes are used as a means of determining the instar of the larvae. These measurements for each instar fall within a small range and these do not overlap. In *W. smithii*, the head capsule measurements of field-collected larvae are as follows:

Instar I	.237±.020 mm.
Instar II	.355±.028 mm.
Instar III	.615±.042 mm.
Instar IV	.857±.100 mm.

This is based on a sample size of n=1204 collected at various times during 1969 at the Kenora site. Because of the distinct difference of head capsule sizes, the various instars were easily separable and identifiable.

(vi) Overwintering

W. smithii exhibits a true larval diapause, overwintering as a third instar larva, encased in the ice cores of the pitchers. When the cores are removed from the pitcher, the larvae can be seen in a curled position in the lower portion of the core, above the main body of the collected debris (Fig. 70) as noted by Smith (1902).

Of 1491 larvae collected on three different occasions during the winter of 1970-1971, all were third instar except for ten dead fourth and one dead second instar. That overwintering takes place in the third instar was further substantiated by collections taken in late fall and early spring at all sites.

Larval mortality is possibly highest during the winter (about 50% at the Pinawa, Telford, and Kenora sites; 65 to 75% at The Pas). The mean number of larvae per leaf taken in the spring and fall of 1969 and 1970 at the various sites, is given in Table 11. The percent survival of larvae collected on three occasions at Pinawa during the winter of 1970-1971 and on two occasions at Kenora during the winter of 1968-1969, are given in Table 12. Spring collections, if taken late enough will show much higher survival rates as the digestive action of the fluid rapidly dissolves those larvae killed during the winter. From the results, it would appear that during the winter the mortality is uniform and continuous. The supercooling temperatures and survival of the larvae at various sub-zero temperatures are discussed in Chapter 6.

(vii) Seasonal abundance in the field

Following the spring thaw, development of the larvae proceeds to fourth instar as soon as the temperature will allow. During April and early May, the larvae are subjected to shorter and shorter recurrent periods of freezing. By the end of May, mean temperatures are sufficiently high (above 15°C) to allow development to proceed uninterrupted (see Chapter 6, Fig. 60). By the end of May and throughout the month of June, most have molted to fourth instar. Toward the end of June and early July, the majority have molted to the pupal stage and some to adults. At this same time eggs and first instar larvae begin to appear in the new leaves which are emerging and opening. The

Table 11

Mean number of larvae per leaf collected in the spring and fall of 1969 and 1970 at the various sites

Year	Location	Spring	Fall
1969	Pinawa	8.40	16.04
	Kenora	17.00	28.35
	Telford	4.75	10.59
	The Pas	1.25	8.71
1970	Pinawa	8.86	19.84
	Kenora	15.7	-
	Telford	-	-
	The Pas	2.24	8.16

Table 12

% survival of larvae collected at two locations during the winter

Date	% Survival Pinawa 1970-71	Kenora* 1968-69
Oct. 8	100	100
Nov. 10	-	82.4
Dec. 29	69.0	-
Jan. 29	54.8	-
Feb. 15	-	52.0

* Smith and Brust, 1971

occurrence of the adult stage appears to coincide with the opening of the new leaves. First instar larvae are prevalent throughout July and into August, whereas second instars predominate to the end of July and into August. From the beginning of August, third instars predominate. Some will molt to fourths, but the percentage is small (see Table 13). The population remains at this stage until the following spring (Fig. 87 to 90). The duration of each stage is shown diagramatically in Figure 91. These figures are based on actual collections taken in 1969 and 1970 and are summarized in Appendix B.

(viii) Number of generations per year

The presence of fourth instar larvae, pupae, and adults from new leaves in late July and August suggests the possibility of two generations per year. Since the preferred oviposition site of adults is new leaves, any fourth instar, pupae, or adults found there could have arisen only from eggs laid that same year. These then represent individuals which may have hatched early in the season and developed to third instar (or beyond the stage that is receptive to diapause-inducing photoperiod) prior to the onset of limiting environmental conditions (see Chapter 5). It is also possible that these represent a small percentage of larvae which develop regardless of restrictive photoperiod (this occurred in laboratory rearings). The majority of larvae (97%) develop to the third instar but no further until the following spring. Table 13 gives the percentages of the various life stages collected from new leaves on various dates at Pinawa during 1970. From this table, the changes in the population over the season are evident and the accumulation of the third instar shows up well. It can be seen that only a small percentage (about 3%, August 7th collection) of the population progresses beyond the third instar. These individuals could

Table 13

% of various life stages in new leaves - Pinawa 1970

Date	Egg	Larva stages 1	2	3	4	Pupa	Adult*	n
3/7/70	100	-	-	-	-	-	-	70
9/7/70	82.6	17.4	-	-	-	-	-	305
18/7/70	73.6	26.1	0.4	-	-	-	-	802
23/7/70	45.7	37.6	21.5	1.2	-	-	-	497
29/7/70	13.3	12.4	62.5	13.1	0.8	0.8	-	526
7/8/70	17.3	23.6	45.1	10.7	1.1	2.0	0.2	802
13/8/70	6.0	10.9	34.4	40.8	-	0.7	0.5	811
20/8/70	21.6	10.2	44.3	27.0	0.3	0.1	1.0	708
27/8/70	7.4	4.3	32.5	55.4	0.1	-	0.1	967
3/9/70	9.4	4.3	15.7	70.5	-	0.1	-	775
10/9/70	3.3	2.5	11.0	82.8	0.3	-	-	866
16/9/70	6.8	1.3	10.6	81.4	-	-	-	1212
24/9/70	4.3	0.8	9.9	84.9	0.1	-	-	908
1/10/70	1.7	-	7.4	88.0	-	-	-	606
8/10/70	2.7	0.1	7.9	89.1	-	-	-	932
12/12/70	-	-	-	100	-	-	-	236

* Pupal exuvia classed as adults.

contribute a second generation during some years. However, the main population found in the leaves at this latitude is univoltine.

(ix) Growth

Larval growth, in general, is dependent on the environmental temperature, inherent genetic characteristics, and the quantity of quality of food. The abundance and variety of fauna trapped by *S. purpurea* should supply ample food for the larvae of *W. smithii*. No quantitative work was carried out, but the decomposing bodies of the insects caught within the leaves should supply sufficient proteins, fats, carbohydrates, and organic and inorganic compounds for larval nutrition.

Growth rates of larvae increase directly with increases in temperature, and in the field the water temperature in the plant must reach 15°C before larval growth will occur. Because of the small habitat, the larval environment is influenced largely by air temperature. Temperature fluctuations in the plant (in summer) correspond to those of the air (see Chapter 6, Fig. 60, and Appendix B). In the winter, temperature fluctuations in the plant are small and do not follow those of the air. The threshold temperature for development (15°C) is exceeded only during the daytime hours in the early spring and growth to fourth instar proceeds slowly. Growth is more rapid during the summer months (June to August) when water temperature in the plant can be 31.1°C for a five day mean with daily highs of 32.2 to 35.0°C occurring occasionally. Maximum-Minimum Self-Registering Thermometers* left in the fielddduring the summer of 1969 at The Pas and Kenora sites revealed maximum temperature one to two inches below the sphagnum of 44.4°C and 51.7°C respectively. From this, it would appear that *W. smithii* are tolerant of

*Taylor Instrument Co. (Ohio) Inc., Ohio, U.S.A.

high temperatures. Laboratory rearings were carried out at 20°, 25°, 27°, and 30°C without any apparent increase in mortality.

While temperature appears to be a limiting factor of larval development in the spring, photoperiod is the limiting factor of larval growth in late summer. Field-collected larvae taken from the field at the beginning of August (August 7, 1970), when kept under natural photoperiods, few (<5%) would progress beyond the third instar, even though the temperature was suitable for growth (24±3°C). These third instar larvae were in diapause and would not progress beyond this stage until the photoperiod was increased above 14 1/2 hours. These larvae were kept in the laboratory (23° to 26°C) under natural photoperiods from the time of collection (August 7th) until the end of January, 1971. The larvae remained active, but fed little. From about the beginning of December onward, mortality increased sharply. The cause is unknown. The experiment was terminated at the end of January, and none of the larvae had progressed to the fourth instar. Other field-collected larvae were held at third instar at 12L:12D and 20°C for a period of several months, with few progressing to fourth instar. Again there was a sharp rise in mortality after three months.

Using five-day mean sphagnum temperatures for 1969-1970 and a threshold temperature of 15°C, the growth period allowable temperature is about three months (end of May to the end of August/early September). If photoperiod is also considered (on the basis of a critical photoperiod range of 14 1/2 to 16 hours), the growth period is reduced to about two months (end of May to the beginning of August). With a normal generation time of about 1 1/2 months in laboratory cultures, it is likely that *W. smithii* can only produce one generation a season at this latitude.

(x) Duration of instars

Assessing the rate of development in the field is, of course, difficult but on the basis of the field collection, it is apparent that there is only one generation per year. Development does not proceed at a uniform rate even under constant conditions of temperature and photoperiod. In the laboratory, at 17L:7D and 25°C, larval development time varied from 20 to 32 days for 50% to reach the pupal stage. Mean time spent in each instar at the above temperature and photoperiod was as follows:

Instar I	5±1 days
Instar II	6±1 days
Instar III	7±1 days
Instar IV	9±3 days

As in other species, the majority of the time spent in the fourth instar stage (34.3%) with 18.5%, 22.2%, and 25.9% of the time spent in the first, second, and third instars respectively. Under diapause conditions (12L:12D and 20°C) the third instar period is extended by several months. Duration of diapausing third instar in the field is from about the end of August to the end of May of the following year, a total of 9 1/2 months.

C. Pupa

When the time of pupation draws near, the larvae remain suspended at the surface, and cease all unnecessary movement. They become noticeably plump and increasingly turgid. At the onset of pupation, the larva assumes a horizontal position at the surface. The larval skin ruptures along the mid-dorsal line of the thorax and the pupa wriggles free. The entire process takes no longer than ten minutes. No diurnal cycle of pupal emergence has been observed.

The newly emerged pupa is translucent on emergence and gradually

darkens with age. Prior to the emergence of the adult, many of the adult characteristics are visible through the pupal skin.

Unlike the pupae of most insects, the pupae of mosquitoes are highly motile, using a pair of large paddles at the end of the abdomen for swimming. *W. smithii* flexes the abdomen rapidly when disturbed and this results in a tumbling action, spiralling the pupae downwards. When the movement stops, the pupae rise to the surface. If undisturbed, the pupae will remain motionless, usually against the side of the pitcher leaf, or pupal container in the case of laboratory cultures. It is likely that little movement of the pupae occurs in the field, unless disturbed by rain drops or the passing of an animal.

The time spent in the pupal stage is an inverse function of temperature (Clement, 1963; Bates, 1949). At 18L:6D and 27°C, the mean pupal period is 6±1 days and agrees with that found by Price (1958). In the field, the pupal period is much more variable, lasting anywhere from 3 to 20 days (see also Judd, 1959). Pupae are most prevalent in the field from mid-June to the end of July, but may be found as late as early September (Fig. 87 to 91).

Prior to the emergence of the adult, the abdomen of the pupa straightens, and becomes horizontal with the water surface. At this time there is little or no movement, even when disturbed.

D. Adult

(i) Emergence

Once the pupal skin has split, the adult swallows air, which slowly distends the stomach, forcing the adult up and out of the pupal exuvia. The swallowed air disappears from the stomach within 24 hours. Adult emergence takes about 5 to 15 minutes and in the field usually occurs at the side of the pitcher leaf. The emerging adult is able to move up onto

the side of the leaf, just above the water line. Here it remains for a variable period of time, probably until the wings can be extended to their full size. Within an hour, the adults are capable of flight and usually move to another location, either within the same leaf, another leaf, or the surrounding vegetation. Emergence can also occur in "open" water. In this case, the emerging adult may remain on the water surface until ready for flight or move across the surface to the side of the container and then up onto the side above the water line.

(ii) Occurrence in the field

Adults can be found in the field from about the end of June, early July, through to about mid-September, being most prevalent during July and August. Adults are most active during the daylight hours, from about 10:00 to 11:00am, with activity peaking in the early afternoon, then decreasing until about 6:00 to 7:00pm. Collection times between sunrise and 10:00am, and 7:00pm and sunset resulted in no adults being observed or captured. Light traps set out overnight in the bog area contained no adult *W. smithii* although other species were trapped.

(iii) Adult flight behavior

Because of their non-biting habits and reluctance to fly unless disturbed, adults are not readily observed or captured in the field. A good portion of the adult's time is spent resting within the mouth of the pitcher plants (Fig. 71), usually in zones 1 and 2, or in the surrounding vegetation (Fig. 72). In flight, adults confine their movements to short, hovering flights from one pitcher to the other or into and out of the vegetation. Adults were never observed to fly above the shrubbery and most excursions were carried out within the undergrowth, rather than the clear areas. This made caputre difficult, and their movements were almost

impossible to trace except over short distances.

Adults can also be observed to "hover" over the mouth of the pitcher for short periods, sometimes descending down into the pitcher cavity, itself, disappearing from view, then returning to the opening (Fig. 73). They often continue this hovering behavior, moving from pitcher to pitcher, then disappearing back into the undergrowth (Fig. 74). Some will move in and out of several pitchers, finally coming to rest within the mouth of one of them. On several occasions, several adults could be seen hovering in and out of the same pitcher. This flight pattern can be duplicated in the laboratory, using artificial pitchers made of glass vials wrapped with black tape, and filled with distilled water (Fig. 75).

Because the sexes of this species are indistinguishable without close examination, it was difficult to tell whether males or females or both exhibit this behavior. Capture was carried out with the use of an aspirator and kept separate on the basis of those captured in flight (including hovering) and those captured resting in the mouth of pitchers (or nearby shrubbery). In the laboratory, collections were sexed, females dissected and the number of follicle (or eggs), stage of ovarian development, and presence of sperm in the spermatheca noted.

The results of the collections (259 adults) showed that the sex ratio of those captured in flight was 72.3% males to 27.7% females. Of those captured, 80.5% were taken while in flight, with 19.5% taken while resting. On the other hand, 47.7% of the females captured were taken in flight, while 53.3% were caught while resting in pitchers. Collections were conducted on several occasions, to reduce any bias in sex ratio due to different emergence time or location.

Of those taken resting in the pitchers, females predominated, although

there was little difference in the number of females taken in flight over those taken resting. The high ratio of males to females taken in flight suggests that males are more active than females, yet both appear to exhibit similar behavior. The differences in sex ratios and the flight behavior can possibly be linked to three different functions: swarming and/or mating, oviposition, and food seeking.

(1a) Swarming: The capture of high numbers of males over pitchers raised the question as to the possibility of swarm behavior in this species. According to Nielsen and Haeger (1960), " 'Swarming' is the habit in male mosquitoes (and other insects) of exhibiting steriotyped flight characterized by performance: (1) within narrow spatial limits; (2) at a certain hour of the day-night cycle (the diel), usually at dusk but also at the dawn in many species; (3) every day of the life span of the adult male beyond the first or the first few days; and (4) at certain places used by males of the same species generation after generation. 'Swarm' is the manifestation of the habit; usually a number of males swarm together but a swarm may consist of very few or even a single individual."

Application of this definition to the hovering behavior of *W. smithii*, coupled with the high ratio of males, perhaps favours the possibility of swarming behavior. (1) The hovering flights are carried out "within narrow spatial limits", that is, in and above the pitcher mouths (or vials in the case of laboratory cultures). The open mouth of the pitcher may act as a swarm marker (see Downes, 1969; Nielsen and Haeger, 1960). (2) Hovering flights by adults do not appear to be restricted to a particular period of the day, although the frequency of occurrence appears to be greatly increased in the early afternoon, when both light intensity and temperature are greatest. (3) Although it is not known whether or not adults exhibit this behavior every

day of their adult life, it has been observed on every collection date. (4) The behavior is exhibited only over the open pitcher leaves. The flight behavior has been produced by both single adults and by several adults together. The occurrence of females taken in flight over pitchers can be explained by the fact that females as well as males may be attracted to swarm-markers (Downes, 1958).

(1b) Mating: Mating may or may not be considered a part of swarming behavior, although mating can occur in swarms. "Copulation in mosquitoes", reports Bates (1949), "seem almost invariably to be associated with the 'swarming' of the males". In *W. smithii*, males have been observed to carry out this hovering flight above and near females resting within the pitchers. The presence of a female, however, did not appear to be necessary for this expression of behavior. In several cases, males attempted to copulate with the female unsuccessfully. On other occasions copulation was achieved.

Females have been observed to copulate with more than one male and on one occasion a single female copulated four times within the space of half an hour. More than one male may attempt copulation with a single female at the same time and up to three have been observed. Copulation has only been observed in resting individuals in this species; and in the field, only within the mouth of the pitcher leaves. Usually it takes place with females resting in older (mature and/or overwintered) leaves. Mating was observed most frequently at the height of adult activity.

Prior to copulation, the female can be found resting either in zone 1 or 2, head up and body projected outward at an angle (about 30°) from the plane of the surface on which she rests. The male approaches from behind, hovering above and around the female for a variable period of time before attempting to copulate. The hovering is so close that contact with the female

may be made, although it is not known if this is part of the mating sequence. The male then grasps the female from behind, rotates until suspended below the female. At the same time, the genitalia are brought into position and contact is made with the genitalia of the female. The pair may remain in copulation for 15 to 30 seconds, after which the male releases and flys off. The female usually retains her position within the leaf and may be subsequently mated again. However, if disturbed, the female may fly off either to a nearby leaf or into the undergrowth.

Of a total of 106 females captured, 95% had sperm in one or more of the three spermathecae, regardless of whether they were caught in flight, hovering, or at rest.

(2) Oviposition: Another possible function of the hovering flight in female is the selection of oviposition sites. *W. smithii* are known to prefer new leaves and these hovering flights have also been observed in and over new leaves. In leaves in which the fluid level was high enough to force females to lay their eggs on the water surface, oviposition behavior could be observed. Ovipositing females usually deposited their eggs on the fluid surface while holding onto the side of the leaf, with only the meta-thoracic legs and possibly the tip of the abdomen touching the surface of the fluid. In the laboratory, females will oviposit while resting on the water surface or on the side of the container. Eggs are laid singly, and often a series of eggs are laid in one place. Oviposition appears to occur both during the day and night in the laboratory. In the field, a preference was shown for the early afternoon.

In 1969, several artificial pitchers (glass vials, see Chapter 3) were placed in the field in an attempt to see if *W. smithii* would oviposit in them. Periodic checks of these vials showed that adults frequent them

(Fig. 76), but they did not oviposit in them. Out of 16 vials in the field, only one larva was found.

Oviposition in laboratory cultures began 5±1 days after emergence and continued as long as females were present in the colony. Duration of egg laying in any individual female was quite variable although most females laid their eggs within three days after the eggs matured.

(3) Food seeking: Carbohydrates extend adult life but are not necessary for the maturation of eggs (Price, 1959; Smith and Brust, 1971). At 18L:6D and 27°C, adult males lived an average of 2.1±0.6 days when denied sugar solution, whereas those fed freely on sugar solution lived 12.5±4.9 days. Adult females lived longer than males, surviving 8.4±0.7 days when denied sugar solution and 24.9±2.1 days when fed. Several carbohydrate sources have been used in the maintaining of adults of *W. smithii*, including sugar solution, honey, raisins, and apples.

In the field, the adults can be observed to actively probe about the nectar-secreting region (zone 1 and 2) of the pitcher leaf. This is particularly true in new leaves, in which secretory action is high. The hovering action exhibited by adults may also be related to searching for a nectar source.

(iv) Ovarian development

Unlike other autogenous mosquitoes, *W. smithii* is precocious and emerges with the follicles already developed to stage IIIa (after Clements, 1963, page 173). Follicular development begins during the life of the pupa. Development is completed in about three to four days at 23°C. The time required to reach the various ovarian stages is given in Table 14, and shown in Figures 78 to 83. Excellent reviews of follicular development are given by Clements (1963) and Detinova (1962).

Development of the follicles generally progresses uniformly but in some cases there is evidence of follicle reabsorption (Fig. 84, 85).

The abundant fat body in adult females at the time of emergence is rapidly depleted as follicle development proceeds to maturity. By the time the follicles reach stage V, most of the fat body has been used.

W. smithii shows some development of the penultimate (secondary) follicle. By the time the primary follicles have reached stage V, the penultimate follicles are at stage IIa to IIb. In a few cases, the development may reach stage IIIa (Table 14 and Fig. 85). The hormonal balance for a second gonotrophic cycle appears to be present, even though most of the fat body is utilized in the development of the first cycle. In the limited number of observations made, there does not appear to be sufficient reserves for the development of the second cycle. Also, in the laboratory, and perhaps in the field, most adult females die after first cycle oviposition, and this may be the limiting factor.

In field-caught adults, all stages of ovarian development were represented. There appeared to be only slight differences in the development of adults caught in flight and those taken resting in pitchers. The percent of follicular development for each of the two groups as well as the combined developmental stages is given in Table 15. Those caught in flight appear to be slightly advanced in follicular development.

(v) Fecundity

In a sample of 60 field-caught females, the mean potential fecundity* per female was 35.0±19.2 eggs. No significant difference was noted between resting female (31.9±23.0, n=56) and females caught in flight (15.2±15.8, n=48).

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*Calculated on the basis of those with stage IIIb development.

Table 14

Ovarian development in *Wyeomyia smithii* reared at 18L:6D/23°C

Maximum Time (in hrs.) After Emergence	n	Developmental Stage* Prinary Follicle	Secondary[1] Follicle	Mean No. of Prinary Follicles
6	28	IIIa	Ia-Ib	61.9 19.6
12	16	IIIa-IIIb	Ib	64.6 22.1
24	26	IIIb	Ib-IIa	35.5 19.0
48	32	IVa	IIa	43.2 23.2
72	30	IVb	IIa-IIb	27.8 15.0
96	32	V	IIa-IIb (IIIa)[2]	35.9 26.2
120	10	V	IIa-IIb	-
142	10	V	IIa-IIb	-

* After Clements (1963) pp. 173.

1 Penultimate follicle.

2 One showed 2nd follicle development beyond stage IIb.

Table 15

Comparison of % development in the various follicle stages between females taken resting and those caught in flight, Pinawa 1970

Condition	n	Developmental Stage IIIa	IIIa-IIIb	IVa-IVb	V	No Eggs
Resting	66	10.6	36.4	24.2	12.1	16.7
In flight	46	4.3	19.6	43.5	21.8	10.9
Combined*	145	6.9	26.9	31.7	20.7	13.8

* Includes some females where the adult condition was not recorded.

In a sample of 92 laboratory-reared females, the mean count was 45.4±24.4 per female. This agreed well with the fecundity of 51.5, n=42 reported by Price (1958). The range of eggs found was similar and varied from as low as one to as high as 98, indicating that high egg production is possible in *W. smithii*

(vi) Sex ratios

The ratio of males to females in field populations at the various study sites appeared to be equal. Larvae collected in the field as third instar were reared through to pupae and their sex noted. The ratios percent are give in Table 16.

E. Population Changes

(i) Annual life stage changes

Weekly sampling of *W. smithii* populations at Pinawa, Telford, and Kenora sites during 1969 and at Pinawa during 1970 show that repeated changes in the population occur at given periods of the year. The occurrence (expressed as frequency percent) of the various life stages in these study areas is shown in Figures 87 to 90. When first sampled in the early part of the season, only third instar larvae (overwintered) can be found. By the end of May, early June, many of the overwintered thirds have molted to fourth instar; a few may have even reached the pupal stage. From mid-June to mid-July most have progressed to the pupal stage and to adults. Eggs begin to show up in the new leaves toward the end of June, followed closely by first instar larvae. First instar larvae are common throughout July, while second instar predominate during August. From early August, the occurrence of third instar increases until, by the middle or end of September, only thirds can be found. These overwinter until the following May.

Table 16

Sex ratios of field-collected larvae (3rd instar) reared to pupae at 18L:6D/27°C

Location	Date	n	% Males	% Females	% Survival
Pinawa	May 11/70	110	51.9	48.1	94.5
	May 11/70	-	54.7	45.3	-
	Sept. 5/70	200	52.6	47.4	98.0
Kenora	May 3/70	105	50.0	50.0	91.4
	May 3/70	-	54.9	45.1	-
The Pas	May 13/70	107	52.8	47.2	67.3
	May 13/70	-	55.6	44.4	-
Telford	Aug. 29/70	200	56.1	43.9	77.5

(ii) Duration of life stages

The functional growth period of *W. smithii* is relatively short, probably no longer than about two months, being regulated both by temperature and photoperiod. The longest life stage in *W. smithii* under field conditions at this latitude is the third instar, lasting approximately 9 1/2 months (Fig. 91). Much of this period is spent encased in the ice cores of the pitcher leaves (5 1/2 to 6 months, that is, the end of October to the end of April). During the other 3 1/2 to 4 months, the larvae is free and active, but little or no growth is exhibited (part of May, all of August, September, and October). In any given year, two generations are represented; the overwintered generation (previous year's eggs) occurs from spring through to July in the overwintered leaves, while the current generation can be found in new leaves from July onward.

Once environmental conditions are suitable, overwintering third instar larvae molt to fourth instar. Fourth instar larvae can be found in overwintered leaves from about the beginning of June through to the end of July. Their occurrence in new leaves is rare, although a few may be found up to mid-September (Table 13).

Pupae are present for a short time only. They can be found in both overwintered and new leaves (although infrequent in the latter) from about mid-June through to mid-September, a period of about four months. The period of highest frequency (mode) is the month of July.

Adults occur in the field from about the end of June to the middle of September, a period of 3 1/2 months. Their appearance coincides with the opening of new leaves of *S. purpurea*.

Eggs can be found as long as adults are present. They can be found in both overwintered and new leaves, but new leaves are preferred oviposition sites.

(iii) Population size in leaves

During the period of study, an unanswered question was whether there was any relationship between the number of larvae and the size of the leaf. While larval populations within leaves may be variable on the basis of leaf size, variation can also be expected to occur with the time of year in which the sample is taken. During the growth period of *W. smithii*, it is difficult to get a reasonable estimate of the possible numbers per leaf as the population is constantly changing. Individuals are constantly leaving the overwintered leaves as adults, and being added to the new leaves as eggs. Thus, if samples are taken when the population is static (late spring or early fall) a more accurate estimate can be made. Two samples were taken from the Pinawa bog during the spring (104 leaves) and fall (206 leaves) of 1970. The results of these samples indicate that a significant linear relationship exists between the size of the leaf and the number of larvae contained within the leaves. The relationship is expressed graphically in Figure 92. The sample taken in the fall of 1970 is perhaps more representative of the relationship as very little mortality had occurred. In the spring sample, winter mortality (50%) must also be considered.

(iv) Population change from old leaves to new leaves

During June and July, two generations exist simultaneously. This is the time of population transfer in which the old habitat (overwintered leaves which will decay by the end of July) is left behind and the new habitat (current year's leaves) is successfully inhabited. The total number found in old leaves in spring is considerably lower than those of the new leaves in fall. This is a result of mortality resulting from the sub-zero temperatures experienced during the winter. Changes in populations at the Pinawa, Telford, and Kenora sites for 1969 and at Pinawa during 1970 are shown in Figure 93. Similar trends are shown at all locations, with the population larger in the fall.

Chapter 8

SUMMARY

1. The literature relating to *W. smithii* was reviewed and found to be limited in relation to the bionomics of this species. It was concluded that this was because *W. smithii* is a species of relatively little economic importance.

2. The pertinent literature relating to insectivorous plants and in particular, the Sarracenians and their insect associates was reviewed and the general aspects of these plants presented. A tabular list of the various species of Sarracenia and their insect associates has also been given.

3. The life cycle of the Pitcher Plant, *S. purpurea* was presented. Leaves, which form the sole habitat of *W. smithii*, begin to grow in the late summer, become dormant through the winter, and emerge the following spring. The leaves mature by the end of June/early July and persist until the following summer. Like the leaves, the flowers begin growth in late summer, become dormant through the winter, emerge the following spring and mature by the end of June/early July. Fluid retention within the leaves forms the habitat for *W. smithii*.

4. The flora of four typical habitats of *S. purpurea* were examined and found to be similar. The Pinawa Bog was looked at in greater detail. A check list of the species present and their spatial distribution has been presented. A possible relationship between tree density, moisture, and

the occurrence of *S. purpurea* was suggested.

5. The geographical distribution of *S. purpurea*, both in Canada and in North America as a whole, was investigated. New maps of its presently known distribution both in Canada and in North American have been included.

6. Fauna, other than *W. smithii*, associated with *S. purpurea* at this latitude were collected and briefly discussed.

7. Characteristics of diapausing *W. smithii* larvae were examined. Respiration rates differed between larval instars, but no differences were detected between diapausing third instar larvae and non-diapausing third instar larvae. The true diapause respiration rate may have been affected by the fact that the diapausing third instar larvae had been held prior to treatment at 12L:12D and 20°C for several weeks. Had diapausing larvae been tested directly upon collection, respiration rates may have differed from non-diapausing larvae.

   Differences in feeding rates were found between diapausing larvae collected in the field, diapausing larvae reared in the laboratory, and non-diapausing larvae reared in the laboratory. The first group fed considerably less than the latter two groups. Uptake rates of radiocesium (^{137}Cs) were also investigated. Differences between diapausing and non-diapausing larvae (^{137}Cs uptake rates) were detected within one hour when larvae were fed labeled dog food (18L:6D and 27°C). Differences in ionic uptake of ^{137}Cs were noted between diapausing and non-diapausing larvae up to six hours after being placed in a nutrient-free ^{137}Cs media.

No significant differences could be detected after six hours.

8. Induction of diapause in *W. smithii* was found to occur when larvae were reared at 16 hours light per day or less at 25°C. One hundred percent induction of diapause occurred at 14 1/2L:9 1/2D per day. The stages receptive to short photoperiods were found to be first instar and early second instar larvae. Larvae reared to third instar at a long-day photoperiod (18L:6D and 27°C), then placed at short photoperiod, continued development uninterrupted regardless of the photoperiods. Above 16 1/2 hours light per day, larval development proceeded to the pupal stage regardless of the stage in which it was started.

9. Diapause, once induced, could be maintained in third instar larvae for several months by holding the larvae at short photoperiod (less than 14 hours light per day at 20°C). Reducing the temperature at which diapausing larvae were held increased the holding time.

10. Diapause was readily terminated by placing larvae under non-diapause photoperiod (greater than 14 1/2 hours light per day). A photoperiod of 0L:24D at 20°C appeared equally effective in terminating diapause.

11. The photoperiod experienced by field populations (Pinawa Bog, 50°15'N) ranged from eight hours on December 21 to a maximum of 16 1/2 hours on June 21. In field populations diapause was terminated about mid-April and induced about mid-August (based on a critical photoperiod of 14 1/2 hours light per day). Spring temperatures, however, delayed development for about a month.

12. The temperature growth threshold in third instar larvae was 15°C, below this, little or no growth occurred.

13. Cold tolerance and supercooling studies revealed that *W. smithii* third instar larvae (the overwintering stage) possessed no distinctive ability to survive sub-zero temperatures. Less than 50% survived when held at -5°C for eight weeks. The larvae did not supercool below -5°C.

14. Snow cover was undoubtably instrumental in the winter survival of *W. smithii* at this latitude. It provided sufficient insulation to prevent the larvae from reaching critically low temperatures, except for short periods (12 hours). During 1969-1970 the lowest five-day mean temperature was about -6°C. The insulating effects of the snow cover also minimized the extremes in daily air temperature changes.

15. Several aspects of the bionomics of *W. smithii* were investigated. At this latitude only one generation per year is possible due to the restrictions placed on the population by photoperiod (14 1/2 hours light per day) and temperature (15°C). These limit the seasonal development time to about two months (end of May to beginning of August). Winter survival studies indicated that only about 50% of the fall population survived the winter. Development time of each larval instar and the pupal stage have been presented. Seasonal changes and duration of various life stages were discussed and illustrated. Population transfer from leaves of the previous year's growth to leaves of the current year's growth was examined. Several aspects of the biology of each life stage were discussed and illustrated. Adult behavior in

the field and in the laboratory has been compared.

16. Ovarian development was examined and illustrated by photomicrographs. All females examined were found to be autogenous.

APPENDIX A - TABLE I

Summary of *Sarracenia purpurea* L. leaf collections, Pinawa Bog 1969-1971

Date	Sample Size	Sample Age[1]	Mean Leaf Size (ml)	Total Larvae	Mean Larval No.	LARVAL INSTAR 1	2	3	4	Dead	PUPAE ♂	♀	ADULT[2] ♂	♀	Total Egg	Mean Egg No.
9/5/69	10	0	31.2	84	8.4	-	-	84	-	-	-	-	-	-	-	-
	-	0	-	67	-	-	-	67	-	-	-	-	-	-	-	-
10/6/69	-	0	-	70	-	-	-	6	64	-	-	-	-	-	-	-
17/6/69	9	0	29.55	80	8.89	-	-	3	76	-	1	-	-	-	-	-
	-	0	-	83	-	-	-	2	79	-	2	-	-	-	-	-
24/6/69	12	0	28.83	92	7.67	-	-	6	81	-	5	-	-	-	-	-
	-	0	-	54	-	-	-	4	42	-	6	2	-	-	-	-
1/7/69	11	0	29.45	115	10.45	-	-	2	102	-	7	3	1	-	-	-
	-	0	-	58	-	-	-	-	51	-	4	3	-	-	-	-
8/7/69	-	0	-	93	-	-	-	3	79	-	7	4	-	-	-	-
15/7/69	25	0	-	121	4.84	-	-	3	78	-	24	16	-	-	-	-
22/7/69	8	N	-	93	11.63	50	43	-	-	-	-	-	-	-	87	10.89
	25	0	-	137	5.48	-	2	1	106	-	16	6	2	4	-	-
29/7/69	14	N	16.21	27	1.93	18	9	-	-	-	-	-	-	-	230	16.28
	25	0	-	68	2.72	3	38	-	25	-	-	2	-	1	-	-
5/8/69	10	N	21.60	14	1.40	6	8	-	-	-	-	-	-	-	153	15.30
	17	N	-	104	6.12	3	39	3	48	-	8	3	-	-	-	-
14/8/69	5	N	17.0	40	8.0	10	30	-	-	-	-	-	-	-	42	8.40
	16	N	-	220	13.75	5	97	117	-	-	-	1	-	-	-	-

[1] N = Current year's leaves
O = Overwintered leaves

[2] Pupal exuvia classed as adult.

APPENDIX A - TABLE I (continued)

Date	Sample Size	Sample Age	Mean Leaf Size (ml)	Total Larvae	Mean Larval No.	LARVAL INSTAR 1	2	3	4	Dead	PUPAE ♂	♀	ADULT ♂	♀	Total Egg	Mean Egg No.
23/8/69	7	N	25.28	22	3.14	-	-	-	-	-	-	-	-	-	205	29.29
	20	N	-	226	11.3	1	150	75	-	-	-	-	-	-	-	-
26/8/69	25	N	-	345	13.80	10	190	145	-	-	-	-	-	-	-	-
1/9/69	25	N	-	401	16.04	-	5	396	-	-	-	-	-	-	-	-
11/5/70	15	0	26.6	133	8.86	-	-	117	-	16	-	-	-	-	-	-
1/6/70	44	0	29.89	257	5.84	-	-	94	161	2	-	-	-	-	-	-
8/6/70	42	0	22.67	49	1.07	-	-	2	43	-	4	-	-	-	-	-
18/6/70	25	0	32.68	166	6.64	-	-	15	130	-	12	9	2	2	-	-
26/6/70	23	0	34.73	113	4.91	-	-	3	97	1	7	5	-	1	-	-
	12	N	15.0	-	-	-	-	-	-	-	-	-	-	-	-	-
3/7/70	26	0	29.08	87	3.35	-	-	1	62	1	9	7	3	5	-	-
	16	N	17.94	-	-	-	-	-	-	-	-	-	-	-	70	4.38
9/7/70	27	0	37.7	110	4.07	-	-	1	86	-	13	3	2	4	-	-
	17	N	39.0	53	3.12	51	-	-	-	2	-	-	-	-	252	14.85
18/7/70	41	0	35.98	223	5.44	37	49	4	76	1	20	20	10	7	-	-
	19	N	33.79	212	11.16	209	3	-	-	-	-	-	-	-	590	31.05
23/7/70	26	0	37.69	249	9.58	67	50	2	69	8	31*		27*		16	0.62
	18	N	29.5	270	15.0	187	107	6	-	-	-	-	-	-	227	12.61

* Sex not noted.

APPENDIX A - TABLE 1 (continued)

Date	Sample Size	Sample Age	Mean Leaf Size (ml)	Total Larvae	Mean Larval No.	LARVAL INSTAR 1	2	3	4	Dead	PUPAE ♂	♀	ADULT ♂	♀	Total Egg	Mean Egg No.
29/7/70	39	0	29.5	66	1.69	6	26	8	16	-	5	3	1	2	-	-
	21	N	27.62	456	21.70	65	329	69	4	-	3	1	-	-	70	3.33
7/8/70	32	N	34.75	663	20.72	189	362	86	9	-	11	5	1	1	139	4.34
13/8/70	38	N	31.39	772	19.00	88	279	331	-	-	2	4	2	2	49	1.28
20/8/70	33	N	31.15	555	16.81	72	313	191	2	1	-	1	5	2	153	4.64
27/8/70	37	N	32.27	895	24.19	42	314	536	1	-	-	-	-	1	72	1.95
3/9/70	38	N	30.68	702	18.47	33	122	546	-	1	-	1	-	-	73	1.92
10/9/70	39	N	32.46	837	21.46	22	95	717	3	-	-	-	-	-	29	0.74
16/9/70	36	N	34.97	1130	31.38	16	128	987	-	-	-	-	-	-	82	2.27
24/9/70	39	N	32.18	869	22.28	7	90	767	1	4	-	-	-	-	39	1.0
1/10/70	36	N	30.31	596	16.56	-	45	533	-	-	-	-	-	-	10	0.36
8/10/70	37	N	30.22	907	24.51	1	74	830	-	-	-	-	-	-	25	0.68
12/12/70	25	N	21.92	236	9.44	-	-	18	-	218	-	-	-	-	-	-
	22	N	26.59	239	10.41	-	-	28	-	201	-	-	-	-	-	-
29/12/70	47	N	27.26	593	12.62	-	-	410	-	184	-	-	-	-	-	-
28/1/71	25	0	-	423	16.92	-	-	232	-	191	-	-	-	-	-	-

APPENDIX A - TABLE II

Summary of *Sarracenia purpurea* L. leaf collections, Kenora Bog 1969-1970

Date	Sample Size	Sample Age[1]	Mean Leaf Size (ml)	Total Larvae	Mean Larval No.	LARVAL INSTAR 1	2	3	4	Dead	PUPAE ♂	♀	ADULT[2] ♂	♀	Total Egg	Mean Egg No.
22/5/69	-	0	-	27	-	-	-	18	9	-	-	-	-	-	-	-
3/6/69	12	0	31.0	204	17.0	-	-	9	179	-	8	8	-	-	-	-
6/6/69	-	0	-	59	-	-	-	1	58	-	-	-	-	-	-	-
	-	0	-	120	-	-	-	-	118	-	2	-	-	-	-	-
12/6/69	10	0	-	115	11.5	-	-	4	109	-	2	-	-	-	-	-
	-	0	-	163	-	-	-	6	157	-	-	-	-	-	-	-
19/6/69	12	0	36.25	92	7.67	-	-	3	87	-	2	-	-	-	-	-
	-	0	-	66	-	-	-	1	65	-	-	-	-	-	-	-
26/6/69	12	0	25.67	56	4.67	-	-	-	56	-	-	-	-	-	-	-
	-	0	-	87	-	-	-	1	79	-	3	2	-	-	-	-
3/7/69	-	0	-	121	-	-	-	1	90	-	21	7	1	1	-	-
10/7/69	26	0	-	138	5.31	-	-	-	119	-	9	6	-	4	-	-
16/7/69	18	0	-	59	3.28	-	-	1	44	-	3	9	1	1	-	-
17/7/69	9	N	-	29	3.22	25	4	-	-	-	-	-	-	-	69	7.67
23/7/69	31	0	-	130	4.19	-	-	-	105	-	16	7	-	2	-	-
	9	N	-	54	6.0	25	29	-	-	-	-	-	-	-	49	5.44

[1] N = Current year's leaves
O = Overwintered leaves

[2] Pupal exuvia classed as adult

Date	Sample Size	Sample Age	Mean Leaf Size (ml)	Total Larvae	Mean Larval No.	LARVAL INSTAR 1	2	3	4	Dead	PUPAE ♂	♀	ADULT ♂	♀	Total Egg	Mean Egg No.
30/7/69	25	0	-	104	4.16	7	30	2	30	-	15	20	-	-	-	-
	11	N	30.27	22	2.0	22	-	-	-	-	-	-	-	-	468	42.55
13/8/69	7	N	27.43	29	4.14	20	9	-	-	-	-	-	-	-	91	13.0
	16	N	-	250	15.63	34	142	74	-	-	-	-	-	-	-	-
22/8/69	12	N	27.83	53	4.42	40	13	-	-	-	-	-	-	-	263	21.92
23/8/69	13	N	-	399	30.69	9	233	157	-	-	-	-	-	-	-	-
29/8/69	7	N	27.30	153	21.86	80	73	-	-	-	-	-	-	-	172	24.57
	18	N	-	627	34.83	8	243	376	-	-	-	-	-	-	-	-
26/10/69	25	N	-	352	14.08	-	-	352	-	-	-	-	-	-	-	-
10/1/70	-	0	-	118	-	-	-	118	-	-	-	-	-	-	-	-
3/5/70	10	0	39.0	157	15.7	-	-	144	-	13	-	-	-	-	-	-
22/5/70	11	0	36.18	163	14.82	-	-	163	-	-	-	-	-	-	-	-
3/6/70	15	0	37.93	89	5.93	-	-	50	39	-	-	-	-	-	-	-
	41	0	24.85	233	5.68	-	-	135	97	-	-	-	-	-	-	-
13/6/70	25	0	43.04	235	9.40	-	-	35	200	-	-	-	-	-	-	-

Summary of *Sarracenia purpurea* L. leaf collections, Telford Bog 1969-1970

Date	Sample Size	Sample Age[1]	Mean Leaf Size (ml)	Total Larvae	Mean Larval No.	LARVAL INSTAR 1	2	3	4	Dead	PUPAE[2] ♂	♀	ADULT ♂	♀	Total Egg	Mean Egg No.
2/6/69	12	0	28.17	57	4.75	-	-	1	51	-	3	2	-	-	-	-
5/6/69	-	0	-	26	-	-	-	1	25	-	-	-	-	-	-	-
11/6/69	10	0	-	108	10.8	-	-	7	98	-	-	-	-	-	-	-
	-	0	-	53	-	-	-	4	47	-	2	-	-	-	-	-
18/6/69	10	0	16.8	82	8.2	-	-	11	63	-	9	2	-	-	-	-
	-	0	-	67	-	-	-	-	57	-	7	3	-	-	-	-
25/6/69	12	0	25.95	58	4.83	-	-	-	49	-	7	2	-	-	-	-
	-	0	-	51	-	-	-	1	46	-	2	2	-	-	-	-
2/7/69	-	0	-	70	-	-	-	1	66	-	3	-	-	-	-	-
9/7/69	54	0	-	133	2.46	-	-	1	93	-	21	9	3	4	-	-
	-	0	-	12	-	-	-	-	11	-	1	-	-	-	-	-
16/7/69	25	0	-	113	4.52	-	-	3	81	-	12	10	4	3	-	-
17/7/69	11	N	-	30	2.73	25	5	-	-	-	-	-	-	-	22	2.0
22/7/69	26	0	-	136	5.23	-	15	3	90	-	13	8	6	1	-	-
	9	N	-	54	6.0	25	29	-	-	-	-	-	-	-	20	2.22

[1] N = Current year's leaves
O = Overwintered leaves

[2] Pupal exuvia classed as adult

APPENDIX A - TABLE III (continued)

Date	Sample Size	Sample Age	Mean Leaf Size (ml)	Total Larvae	Mean Larval No.	1	2	3	4	Dead	PUPAE ♂	PUPAE ♀	ADULT ♂	ADULT ♀	Total Egg	Mean Egg No.
29/7/69	19	0	-	57	3.0	-	1	1	41	-	5	6	2	1	-	-
	9	N	18.89	16	1.78	16	-	-	-	-	-	-	-	-	157	17.44
	21	-	-	138	6.57	15	81	2	33	-	-	7	-	-	-	-
6/8/69	-	-	-	95	-	19	37	6	30	-	2	1	-	-	-	-
	7	N	21.86	66	9.42	22	44	-	-	-	-	-	-	-	10	1.43
	2	N	-	38	19.0	16	22	-	-	-	-	-	-	-	-	-
14/8/69	19	N	-	94	4.95	-	49	48	-	-	-	-	-	-	-	-
	6	N	19.0	23	3.83	10	13	-	-	-	-	-	-	-	11	1.8
23/8/69	8	N	18.0	12	1.5	12	-	-	-	-	-	-	-	-	131	16.38
	24	N	-	194	8.08	3	88	103	-	-	-	-	-	-	-	-
27/8/69	7	N	11.71	21	3.0	7	14	-	-	-	-	-	-	-	75	10.71
	30	N	-	224	7.47	-	61	163	-	-	-	-	-	-	-	-
8/6/70	9	N	17.56	46	5.11	42	4	-	-	-	-	-	-	-	86	9.56
29/6/70	11	N	17.45	161	14.64	11	118	18	14	-	2	3	-	-	33	3.0
21/7/70	10	N	15.6	58	5.8	37	21	-	-	-	-	-	-	-	7	0.7
11/8/70	10	N	22.9	147	14.7	34	61	44	-	-	1	-	-	-	106	10.6

APPENDIX A - TABLE IV

Summary of *Sarracenia purpurea* L. leaf collections, The Pas Bog 1969-1970

Date	Sample Size	Sample Age[1]	Mean Leaf Size (ml)	Total Larvae	Mean Larval No.	LARVAL INSTAR				Dead	PUPAE		ADULT		Total Egg	Mean Egg No.
						1	2	3	4		♂	♀	♂	♀		
15/5/69	12	0	19.58	15	1.25	-	-	-	-	15	-	-	-	-	-	-
6/9/69	14	N	20.21	33	2.36	-	-	33	-	-	-	-	-	-	63	4.5
	33	N	-	348	10.55	1	95	248	1	-	1	-	1	1	-	-
13/5/70	29	0	26.45	65	2.24	-	-	52	-	12	-	-	-	-	-	-
27/9/70	20	N	25.6	176	8.8	-	2	174	-	-	-	-	-	-	8	0.4
	54	N	27.7	367	6.79	-	1	366	-	-	-	-	-	-	21	0.38

[1] N = Current year's leaves
0 - Overwintered leaves

APPENDIX B

Meteorological Summary -- Pinawa Bog (50°15'N), October 1, 1969 to October 18, 1970.

The following comprises a daily summary of the various meteorological records kept during the period from October 1, 1969 through to October 18, 1970 at the Pinawa Bog. Sphagnum temperatures were derived from two recorders placed in the bog during the above period. Air temperatures, rainfall, snowfall, and prevailing winds data was supplied through the courtesy of Mr. A. Reimer, Meteorologist, A.E.C., Pinawa, Manitoba. Sunlight, Civil Twilight data was taken from the Smithsonian Meteorological Tables, Smithsonian Misc. Collection 114. Snow depth records were derived from both A.E.C.L. reports and personal records. Temperatures were recorded in Fahrenheit and later converted to Centigrade as required.

METEOROLOGICAL SUMMARY

Month of October, 1969

Pinawa, Man. A.E.C.L. Site 50°15'N - 95°50'W

Daily Temperatures, Precipitation, Light, and Snow Depth

Day	Sphagnum Max.	Sphagnum Min.	Sphagnum Mean	Air Max.	Air Min.	Air Mean	Rain (in.)	Snow (in.)	Ppt. (in.)	Snow Depth (in.)	Daylight H. m.	Civil Twilight H. m.	Total Light H. m.
1	-	-	-	48	40	44	.11		.11		11:39	32	12:11
2	48.5	41.5	45	49	43	46							
3	49.3	41.3	45.3	54	43	48.5	.26		.26				
4	50.3	41.5	45.9	47	45	46	.03		.03				
5	49.8	33.5	41.1	44	37	40.5	.03		.03		11:24	32	11:56
6	46.0	33.5	39.8	45	36	40.6	.06		.06				
7	42.3	34.8	38.5	42	35	38.5	.31	.03	.34				
8	43.3	30.8	37.0	53	33	43.0							
9	50.5	32.3	41.4	51	35	43.0					11:10	32	11:42
10	40.8	32.8	36.8	39	35	37.0							
11	42.5	31.8	37.1	40	31	35.5	.01	0.1	.02				
12	42.0	29.8	35.9	43	30	36.5							
13	39.5	29.8	34.6	40	31	35.5					10:56	32	11:28
14	32.8	29.0	30.9	38	29	33.5	.06		.06				
15	42.5	32.0	37.3	40	33	36.5	.01		.01				
16	40.3	31.5	35.9	40	27	33.5							
17	34.0	30.3	32.1	40	27	33.5					10:40	33	11:13
18	39.8	28.5	34.1	41	30	35.5							
19	39.8	28.5	34.1	44	25	34.5							
20	32.0	26.8	29.4	33	22	27.5		0.1	.01				
21	31.3	28.0	29.6	30	25	27.5					10:26	33	10:59
22	32.3	20.3	26.3	33	18	25.5							
23	33.8	16.8	25.3	37	15	26.0							
24	34.3	24.8	29.5	36	27	31.5		0.4	.04				
25	30.8	28.5	29.6	33	25	29.0		0.4	.04		10:12	33	10:45
26	30.3	19.8	25.0	27	19	23.0							
27	31.5	19.3	25.4	34	20	27.0							
28	32.5	18.3	25.9	44	20	32.0							
29	34.3	23.5	28.9	43	30	36.5					9:59	33	10:32
30	40.8	33.3	37.0	45	38	41.5	.03		.03				
31	42.3	32.5	37.4	43	35	39.0							
TOTAL							.91	1.03	1.04				
MEAN	38.1	28.6	33.3	41.2	30.3	35.7	.09	.21	.07				

Five Day Mean

Week of	Sphagnum Max.	Sphagnum Min.	Sphagnum Mean	Air Max.	Air Min.	Air Mean
1-5	49.5	39.5	44.3	48.4	41.6	45.0
6-10	44.6	32.8	36.7	46.0	34.8	40.4
11-15	39.9	30.5	35.2	40.2	30.8	35.5
16-20	37.2	29.1	33.1	39.6	26.2	32.9
21-25	32.5	23.7	28.1	33.8	22.0	27.9
25-31	35.3	24.5	29.9	39.3	27.0	33.2

Monthly Temperature Extremes and Mean

	Sphag.	Air
High	50.3	54
Low	16.8	15
Mean	33.3	35.6

Wind

Mean Speed (MPH)	5.9
Prevailing Direction	SSE

Ppt.--Sum of rainfall and 1/10th of snowfall.

All temperatures in degrees F

T--Trace

Daylight--Interval between sunrise and sunset

Civil Twilight--Interval between sunrise and sunset and the time when the true position of the center of the sun is 6° below the horizon. First magnitude stars are just visible.

Total Light--Daylight and Civil Twilight.

Month of November, 1969

METEOROLOGICAL SUMMARY

Pinawa, Man. A.E.C.L. Site 50°15'N - 95°50'W

Daily Temperatures, Precipitation, Light, and Snow Depth

Day	Sphagnum Max.	Sphagnum Min.	Sphagnum Mean	Air Max.	Air Min.	Air Mean	Rain (in.)	Snow (in.)	Ppt. (in.)	Snow Depth (in.)	Daylight H. m.	Civil Twilight H. m.	Total Light H. m.
1	32.3	29.3	30.8	36	27	31.5							
2	39.0	31.8	35.4	37	34	35.5					9:48	34	10:22
3	36.5	30.8	33.6	45	30	37.5							
4	36.3	27.8	32.0	53	28	40.5							
5	45.5	30.3	38.0	53	33	43.0							
6	46.5	30.5	38.5	59	32	45.5					9:35	34	10:19
7	48.5	29.8	39.1	57	30	43.5							
8	50.5	31.3	40.9	56	35	45.5							
9	42.3	36.5	39.4	45	36	40.5							
10	45.3	40.0	42.6	47	40	43.5	.01		.01		9:22	35	9:57
11	39.3	31.0	35.1	35	31	33.0		.3	.03				
12	32.0	27.5	29.8	27	24	25.5		.4	.04				
13	27.0	22.3	24.6	20	11	15.5		.4	.04				
14	26.8	25.3	26.0	21	14	17.5		.6	.06	1.5	9:10	35	9:45
15	27.5	26.0	26.8	20	13	16.5							
16	27.8	22.8	25.3	24	6	15.0							
17	27.5	20.8	24.1	21	17	19.0							
18	25.8	18.5	22.1	15	7	11.0		.6	.06	2.0	8:58	36	9:34
19	26.5	23.3	24.9	16	9	12.5		.2	.02	2.7			
20	26.5	22.0	24.3	17	-3	7.0		.1	.01				
21	29.0	23.0	26.0	29	-1	14.0							
22	26.0	24.5	25.3	19	12	16.0		.8	.08		8:47	36	9:23
23	27.5	22.0	24.8	32	7	19.5							
24	32.0	27.5	29.8	41	21	31.0							
25	32.0	21.0	26.5	17	12	14.5		.3	.03				
26	22.0	21.0	21.5	16	10	13.0				3.0	8:38	37	9:15
27	28.3	14.3	21.3	37	1	19.0							
28	28.3	19.0	23.6	33	19	26.0				2.2			
29	25.8	13.3	19.5	35	0	18.5				1.9			
30	30.0	22.0	26.0	40	29	34.5					8:29	37	9:06
31													
TOTAL							.01	.01	3.7				
MEAN	31.9	26.7	29.3	33.4	18.8	26.1	-	.41	.04				

Five Day Mean

Week of	Sphagnum Max.	Sphagnum Min.	Sphagnum Mean	Air Max.	Air Min.	Air Mean
1-5	37.9	30.0	34.0	44.8	30.4	37.6
6-10	46.6	33.6	40.1	52.8	34.6	43.7
11-15	30.7	26.4	28.5	24.6	18.6	21.6
16-20	26.8	21.5	24.1	18.6	9.2	12.9
21-25	29.3	23.6	26.5	27.6	10.2	19.0
26-30	26.9	17.9	22.4	32.2	11.8	22.2

Monthly Temperature Extremes and Mean

	Sphag.	Air
High	50.5	59
Low	13.3	-3
Mean	29.3	26.1

Wind

Mean Speed (MPH)	7.1
Prevailing Direction	NW

Ppt.--Sum of rainfall and 1/10th of snowfall.

All temperatures in degrees F

T--Trace

Daylight--Interval between sunrise and sunset

Civil Twilight--Interval between sunrise and sunset and the time when the true position of the center of the sun is 6° below the horizon. First magnitude stars are just visible.

Total Light--Daylight and Civil Twilight.

Month of December, 1969

METEOROLOGICAL SUMMARY

Pinawa, Man. A.E.C.L. Site 50°15'N - 95°50'W

Daily Temperatures, Precipitation, Light, and Snow Depth

Day	Sphagnum Max.	Sphagnum Min.	Sphagnum Mean	Air Max.	Air Min.	Air Mean	Rain (in.)	Snow (in.)	Ppt. (in.)	Snow Depth (in.)	Daylight H. m.	Civil Twilight H. m.	Total Light H. m.
1	29.5	18.5	24.0	50	17	28.5							
2	29.8	24.5	27.1	37	30	33.5				1.5	8:24	37	9:01
3	24.5	11.5	18.0	20	11	15.5							
4	25.5	10.0	17.8	26	3	14.5				0.4 nm.			
5	29.5	21.5	25.5	23	20	26.5		1.0	.10		8:17	37	8:54
6	30.0	29.5	29.8	30	27	28.5		1.1	.11				
7	30.5	29.0	29.8	29	25	27.0		2.6	.26				
8	30.5	30.0	30.3	25	23	24.0		.6	.06	4.5			
9	30.0	29.0	29.5	25	21	23.0		.3	.03	5.8	8:12	38	8:50
10	29.0	28.5	29.8	22	18	20.0		.2	.02	5.8			
11	27.3	26.5	27.9	20	15	17.5		.2	.02	5.8			
12	26.3	26.0	26.1	20	11	15.5		1.6	.16	5.4			
13	26.5	26.0	26.3	19	13	16.0		.5	.05		8:08	38	8:46
14	26.3	26.0	26.1	15	9	12.0							
15	28.0	27.5	27.8	25	-7	9.0				6.8			
16	28.0	27.5	27.8	29	13	21.0				6.6			
17	28.5	28.0	28.3	27	19	23.0		.1	.01	6.0	8:06	39	8:45
18	27.3	27.0	27.1	19	14	16.5		.2	.02	6.2			
19	27.0	26.0	26.5	17	10	13.5		T	T	6.3			
20	27.0	26.0	26.5	17	-5	6.0							
21	26.0	25.0	25.5	-1	-10	-5.5					8:04	39	8:43
22	25.0	25.0	25.0	1	-19	-9.0				6.1			
23	25.0	24.0	24.5	17	-13	2.0		.9	.09	6.0			
24	27.0	24.0	25.5	20	7	13.5		.8	.08	7.1			
25	27.0	25.0	26.0	8	5	6.5		T	T		8:05	39	8:44
26	27.0	26.8	26.9	8	5	6.5							
27	28.5	27.0	27.8	10	-5	2.5		.1	.01				
28	27.0	27.0	27.0	14	2	8.0		.8	.08				
29	27.5	27.0	27.3	13	-3	5.0				8.6	8:07	38	8:45
30	27.5	27.0	27.3	16	2	9.0		.5	.05	9.0			
31	28.0	27.0	27.5	18	11	14.5		.4	.05	9.1			
TOTAL								11.9	1.19				
MEAN	27.6	25.27	26.5	20.3	8.7	14.5		.7	.07				

nm. - not measurable

Five Day Mean

Week of	Sphagnum Max.	Sphagnum Min.	Sphagnum Mean	Air Max.	Air Min.	Air Mean
1-5	27.8	17.2	22.5	33.2	16.2	23.7
6-10	30.0	29.2	29.8	26.2	22.8	24.5
11-15	26.9	26.4	26.8	19.8	8.2	14.0
16-20	27.6	26.9	27.2	21.8	10.2	16.0
21-25	26.0	24.6	25.3	9.0	-6.0	1.5
26-31	27.6	27.0	27.3	13.2	2.0	7.6

Monthly Temperature Extremes and Mean

	Sphag.	Air
High	30.5	50
Low	24.5	-19
Mean	26.5	14.5

Wind

Mean Speed (MPH)	5.1
Prevailing Direction	SSE

Ppt.--Sum of rainfall and 1/10th of snowfall.

All temperatures in degrees F

T--Trace

Daylight--Interval between sunrise and sunset

Civil Twilight--Interval between sunrise and sunset and the time when the true position of the center of the sun is 6° below the horizon. First magnitude stars are just visible.

Total Light--Daylight and Civil Twilight.

Month of January, 1970

METEOROLOGICAL SUMMARY

Pinawa, Man. A.E.C.L. Site 50°15'N - 95°50'W

Daily Temperatures, Precipitation, Light, and Snow Depth

Day	Sphagnum Max.	Sphagnum Min.	Sphagnum Mean	Air Max.	Air Min.	Air Mean	Rain (in.)	Snow (in.)	Ppt. (in.)	Snow Depth (in.)	Daylight H. m.	Civil Twilight H. m.	Total Light H. m.
1	26.8	26.5	26.6	20	14	17.0		.2	.02	9.7	8:10	38	8:48
2	26.8	26.5	26.6	9	3	6.0		.4	.04	9.7			
3	26.5	25.8	26.1	5	-3	1.0		.2	.02				
4	27.5	26.0	26.8	-2	-21	-11.5		.2	.02				
5	26.0	26.0	26.0	4	-6	-1.0		.4	.04	10.0	8:15	38	8:52
6	26.0	26.0	26.0	0	-7	-3.5		.5	.05	10.3			
7	26.0	25.0	25.5	0	-13	-6.5		.2	.02	10.8			
8	25.0	24.0	24.5	4	-12	-4.0				10.4			
9	25.0	24.0	24.5	4	-10	-3.0				10.2	8:21	38	8:59
10	25.0	25.0	25.0	18	-13	2.5		1.0	.10				
11	27.0	25.0	26.0	7	2	4.5							
12	27.0	23.0	25.0	-7	-21	-14.0				11.1			
13	23.0	18.0	20.5	-10	-36	-23.0		.2	.02	10.9	8:30	38	9:08
14	22.0	18.0	20.0	-2	-18	-10.0		2.2	.22				
15	24.0	22.0	23.0	-2	-7	-4.5		1.0	.10	15.2			
16	24.0	24.0	24.0	-19	-27	-23.0							
17	24.0	18.5	21.3	-15	-35	-25.0					8:38	37	9:15
18	18.5	18.0	18.8	-12	-34	-23.0							
19	18.0	18.0	18.0	-11	-35	-23.0							
20	18.0	18.0	18.0	-11	-35	-23.0				14.1			
21	19.0	18.0	18.5	-1	-34	-17.5		.1	.01	13.9	8:48	37	9:25
22	22.0	19.0	20.5	2	-10	-4.0		T	T	13.6			
23	23.0	22.0	22.5	17	-24	-3.5		.5	.05	13.4			
24	25.5	23.0	24.3	20	10	15.0							
25	27.5	25.5	26.5	20	13	16.5		T	T		8:59	36	9:35
26	25.5	25.7	25.6	21	13	17.0				13.2			
27	26.9	26.0	26.4	24	8	16.0		T	T	13.1			
28	27.8	24.2	26.0	21	8	14.5				12.8			
29	22.7	22.9	22.8	14	-15	-0.5				12.8	9:11	36	9:46
30	24.5	21.4	22.9	30	6	18							
31	25.5	24.5	25.0	18	9	13.5		1.5	.15				
TOTAL								8.6	.86				
MEAN	24.4	22.9	23.7	5.4	-10.6	-2.6		6.1	.61				

Five Day Mean

Week of	Sphagnum Max.	Sphagnum Min.	Sphagnum Mean	Air Max.	Air Min.	Air Mean
1-5	26.7	26.2	26.4	7.2	2.6	2.3
6-10	25.4	24.8	25.1	5.2	-11.0	-2.9
11-15	24.6	21.2	22.9	-2.8	-16.0	-9.4
16-20	20.5	19.3	20.0	-13.6	-33.2	-23.4
21-25	23.4	21.5	22.5	11.6	-9.0	1.3
26-31	25.5	24.1	24.8	21.3	4.8	13.1

Monthly Temperature Extremes and Mean

	Sphag.	Air
High	27.8	30
Low	18.0	-36
Mean	23.7	-2.6

Wind

Mean Speed (MPH)	4.1
Prevailing Direction	NNW

Ppt.--Sum of rainfall and 1/10th of snowfall.

All temperatures in degrees F

T--Trace

Daylight--Interval between sunrise and sunset

Civil Twilight--Interval between sunrise and sunset and the time when the true position of the center of the sun is 6° below the horizon. First magnitude stars are just visible.

Total Light--Daylight and Civil Twilight.

Month of February, 1970

METEOROLOGICAL SUMMARY

Pinawa, Man. A.E.C.L. Site 50°15'N - 95°50'W

Daily Temperatures, Precipitation, Light, and Snow Depth

Day	Sphagnum Max.	Sphagnum Min.	Sphagnum Mean	Air Max.	Air Min.	Air Mean	Rain (in.)	Snow (in.)	Ppt. (in.)	Snow Depth (in.)	Daylight H. m.	Civil Twilight H. m.	Total Light H. m.
1	25.1	20.4	22.7	6	-18	-6.0		.8	.08		9:20	35	9:55
2	19.5	12.4	16.0	-18	-29	-23.5		T		14.3			
3	14.0	11.3	12.7	-5	-30	-17.5		.3	.03				
4	-	-	-	8	-9	.-0.5		.1	.01	14.3			
5	20.6	16.4	18.5	9	-6	1.5				14.2	9:33	35	10:08
6	22.6	18.1	20.4	31	-15	8.0				14.1			
7	23.1	19.9	21.5	20	-5	7.5		.1	.01				
8	24.5	21.3	22.9	23	5	14.0							
9	27.8	23.6	25.7	32	11	21.5				13.4	9:46	34	10:20
10	28.3	26.0	27.1	17	0	8.5				13.4			
11	26.0	24.1	25.0	10	-1	4.5		.4	.04	13.3			
12	24.1	19.4	21.8	0	-8	-4.0				13.6			
13	19.4	12.4	15.9	-3	-25	-14.0					10:00	34	10:34
14	13.8	10.6	12.1	7	-25	-9.0							
15	13.6	11.5	12.6	4	-25	-10.5		1.7	.17				
16	16.9	11.3	14.1	11	-16	-2.5		.4	.04	15.3			
17	20.3	15.1	17.7	9	-13	-2.0		1.9	.19	20.2	10:15	33	10:48
18	21.7	19.0	20.4	-3	-21	-12.0		.4	.04				
19	22.2	20.8	21.5	-4	-13	-8.5		T	T	19.4			
20	24.7	20.4	22.6	18	-17	0.5		.1	.01	19.1			
21	26.6	22.0	24.3	40	9	24.5					10:28	33	11:01
22	27.8	25.7	26.7	31	19	25.0							
23	29.3	26.4	27.8	35	21	28.0				16.8			
24	28.3	24.8	26.5	12	4	8.0		T	T	16.6			
25	25.8	21.0	23.4	11	-24	6.5		.7	.07	16.4	10:43	33	11:16
26	23.8	22.0	22.9	12	-6	3.0							
27	23.9	20.2	22.0	13	-25	-6.0				16.2			
28	23.4	19.2	21.3	20	-20	0					10:58	33	11:31
29													
30													
31													
TOTAL								6.9	.69				
MEAN	23.2	19.1	21.0	12.4	-10.1	1.2		.63	.063				

Five Day Mean

Week of	Sphagnum Max.	Sphagnum Min.	Sphagnum Mean	Air Max.	Air Min.	Air Mean
1-5	19.8	15.1	17.5	0.0	-18.4	-9.2
6-10	25.2	21.8	23.5	24.6	-0.8	11.9
11-15	19.4	15.6	17.5	3.6	-16.8	-6.6
16-20	21.2	17.3	19.3	6.2	-16.0	-4.9
21-25	29.6	24.0	25.7	25.8	5.8	18.4
26-28	23.7	20.5	22.1	15.0	-17	-1.0

Monthly Temperature Extremes and Mean

	Sphag.	Air
High	29.3	40
Low	11.3	-30
Mean	21.0	1.2

Wind

Mean Speed (MPH)	5.4
Prevailing Direction	NNW

Ppt.--Sum of rainfall and 1/10th of snowfall.

All temperatures in degrees F

T--Trace

Daylight--Interval between sunrise and sunset

Civil Twilight--Interval between sunrise and sunset and the time when the true position of the center of the sun is 6° below the horizon. First magnitude stars are just visible.

Total Light--Daylight and Civil Twilight.

Month of March, 1970

METEOROLOGICAL SUMMARY

Pinawa, Man. A.E.C.L. Site 50°15'N - 95°50'W

Daily Temperatures, Precipitation, Light, and Snow Depth

Day	Sphagnum Max.	Sphagnum Min.	Sphagnum Mean	Air Max.	Air Min.	Air Mean	Rain (in.)	Snow (in.)	Ppt. (in.)	Snow Depth (in.)	Daylight H. m.	Civil Twilight H. m.	Total Light H. m.
1	22.7	19.2	20.9	17	-20	-1.5		.2	.02		10:58	33	11:31
2	23.3	20.4	21.9	25	-6	-9.5		8.5	.85				
3	26.4	23.3	24.8	28	18	23.0	T	1.5	.15	25.4			
4	27.4	22.8	25.1	12	0	6.0		T	T				
5	27.9	25.1	26.4	18	-3	7.5		.2	.02	25.2	11:12	33	11:45
6	26.9	23.3	25.1	9	-10	-0.5				25.0			
7	24.6	20.8	22.7	2	-31	-14.5							
8	24.0	21.8	22.9	14	-3	5.5							
9	24.3	20.4	22.3	15	-18	-1.5				22.4	11:28	32	12:00
10	24.7	20.7	22.7	18	-19	-0.5				22.2			
11	24.3	21.0	22.6	19	-12	3.5				21.9			
12	24.3	21.6	22.9	18	-2	8.0		.4	.04				
13	26.1	23.4	24.7	23	8	15.5				21.8	11:42	32	12:14
14	26.8	23.4	25.1	24	-2	11.0							
15	27.5	23.2	25.4	30	-14	8.0							
16	27.5	23.5	25.5	34	-5	14.5				21.0			
17	28.8	25.7	27.2	43	12	27.5				20.2	11:58	32	12:30
18	29.9	25.5	27.7	43	12	27.5				20.1			
19	30.4	26.7	28.5	42	13	27.5				19.3			
20	30.4	26.8	28.6	43	0	21.5				19.3			
21	32.7	27.7	30.2	43	15	29.0		.2	.02		12:13	32	12:45
22	31.6	30.5	31.0	29	17	23.0							
23	31.6	28.0	29.8	36	-2	17.0				18.7			
24	31.1	24.8	28.0	41	10	25.5		.1	.01	18.5			
25	31.1	29.7	30.4	27	18	22.5		T	T	18.5	12:28	33	13:01
26	30.3	27.4	28.8	17	2	9.5		.4	.04				
27	27.9	23.2	25.5	7	-12	-2.5							
28	25.9	19.8	22.8	13	-15	-1.0							
29	24.2	19.8	22.0	25	-16	4.5		.4	.04		12:43	33	13:16
30	26.4	22.3	24.3	22	5	13.5				18.6			
31	26.8	23.7	25.2	20	-5	7.5				18.6			
TOTAL								11.9	1.19				
MEAN	27.4	23.7	25.5	24.4	-2.1	11.2		1.32	.132				

Five Day Mean

Week of	Sphagnum Max.	Sphagnum Min.	Sphagnum Mean	Air Max.	Air Min.	Air Mean
1-5	25.5	22.2	23.8	20.0	-2.2	5.1
6-10	24.9	21.4	23.1	11.6	-16.2	-2.3
11-15	25.8	22.5	24.1	22.8	-4.4	9.2
16-20	29.4	25.6	27.5	41.0	6.4	23.7
21-25	31.6	28.1	29.9	35.2	11.6	23.4
26-31	26.9	22.7	24.8	17.3	-6.8	5.3

Monthly Temperature Extremes and Mean

	Sphag.	Air
High	30.7	43
Low	19.2	-31
Mean	25.5	11.2

Wind

Mean Speed (MPH)	4.9
Prevailing Direction	NNW

Ppt.--Sum of rainfall and 1/10th of snowfall.

All temperatures in degrees F

T--Trace

Daylight--Interval between sunrise and sunset

Civil Twilight--Interval between sunrise and sunset and the time when the true position of the center of the sun is 6° below the horizon. First magnitude stars are just visible.

Total Light--Daylight and Civil Twilight.

METEOROLOGICAL SUMMARY

Month of April, 19 70

Pinawa, Man. A.E.C.L. Site 50°15'N - 95°50'W

Daily Temperatures, Precipitation, Light, and Snow Depth

Day	Sphagnum Max.	Sphagnum Min.	Sphagnum Mean	Air Max.	Air Min.	Air Mean	Rain (In.)	Snow (in.)	Ppt. (in.)	Snow Depth (in.)	Day-light H. m.	Civil Twilight H. m.	Total Light H. m.
1	27.0	26.5	26.8	30	-4	13.0				18.6	12:55	33	13:28
2	28.0	26.5	27.3	34	18	26.0		.1	.01				
3	29.9	27.3	28.6	29	19	24.0				18.4			
4	30.6	26.7	28.6	39	2	20.5							
5	33.6	29.2	31.4	43	25	34.4		T	T		13:09	33	13:42
6	34.1	32.3	33.2	41	25	33.0				16.8			
7	35.0	32.3	33.6	58	30	44.0	.04	T	.04	13.5			
8	33.6	31.4	32.5	36	19	27.5		1.3	.13				
9	33.2	31.0	32.1	30	10	20.0					13:24	34	13:58
10	33.6	29.3	31.5	36	7	21.5				10.9			
11	33.6	31.8	32.7	45	28	36.0							
12	36.3	32.3	34.3	45	29	37.0				9.1			
13	39.4	32.3	35.8	46	31	38.5				8.2	13:38	34	14:12
14	42.4	33.2	37.8	45	32	38.5				7.0			
15	43.3	33.2	38.5	46	32	39.0	.31		.31	4.6			
16	42.0	34.2	38.1	41	34	37.5	.06	.1	.07				
17	47.4	32.8	40.1	47	30	38.5					13:53	35	14:28
18	50.8	26.0	38.4	48	25	36.5							
19	34.4	32.8	33.6	37	32	34.5		3.5	.35				
20	33.5	33.0	33.2	33	30	31.5		3.5	.35	3.0			
21	33.9	34.0	33.9	34	30	32.0		1.0	.10	4.0	14:07	35	14:42
22	37.8	33.5	35.6	37	31	34.0		0.1	.01				
23	42.6	32.5	37.6	40	31	35.5	T	T	T	2.0			
24	57.6	29.5	43.6	57	26	41.5							
25	62.8	32.1	47.4	57	37	47.0				nm.	14:21	36	14:57
26	61.5	32.5	47.0	57	37	47.0	.05		.05				
27	55.2	31.8	43.5	45	41	43.0	.19		.19				
28	48.6	41.0	44.8	59	39	49.0	T		T				
29	65.5	39.1	52.3	40	35	37.5		T	T		14:34	36	15:10
30	46.4	34.4	40.4	55	31	43.0	.05		.05				
31													
TOTAL							0.65	9.6	1.61				
MEAN	41.1	31.8	36.5	43.0	26.4	34.7	.12	1.37	.257				

nm. - not measurable

Five Day Mean

Week of	Sphagnum Max.	Sphagnum Min.	Sphagnum Mean	Air Max.	Air Min.	Air Mean
1-5	29.8	27.2	28.5	35.0	12.0	23.6
6-10	33.9	31.3	32.6	40.2	18.2	29.2
11-15	39.0	32.6	35.8	45.4	30.4	37.8
16-20	41.6	31.8	36.7	41.2	30.2	35.7
21-25	46.9	32.3	39.6	45.0	49.0	38.0
26-30	55.4	35.8	45.6	51.2	36.6	43.9

Monthly Temperature Extremes and Mean

	Sphag.	Air
High	65.6	59
Low	26.0	-4
Mean	36.5	34.7

Wind

Mean Speed (MPH)	7.97
Prevailing Direction	ENE

Ppt.--Sum of rainfall and 1/10th of snowfall.

All temperatures in degrees F

T--Trace

Daylight--Interval between sunrise and sunset

Civil Twilight--Interval between sunrise and sunset and the time when the true position of the center of the sun is 6° below the horizon. First magnitude stars are just visible.

Total Light--Daylight and Civil Twilight.

METEOROLOGICAL SUMMARY

Month of May, 1970

Pinawa, Man. A.E.C.L. Site 50°15'N - 95°50'W

Daily Temperatures, Precipitation, Light, and Snow Depth

Day	Sphagnum Max.	Sphagnum Min.	Sphagnum Mean	Air Max.	Air Min.	Air Mean	Rain (in.)	Snow (in.)	Ppt. (in.)	Snow Depth (in.)	Daylight H. m.	Civil Twilight H. m.	Total Light H. m.
1	44.8	29.9	37.3	40	23	31.5					14:41	37	15:18
2	59.6	27.1	43.4	64	24	44.0							
3	63.4	32.3	47.8	58	34	46.0							
4	36.9	31.4	34.1	38	28	33.0	T	3.0	.30				
5	51.8	29.9	40.9	48	25	36.5					14:54	37	15:31
6	59.4	33.9	46.6	68	35	51.5	T		T				
7	74.2	38.0	56.1	71	40	55.5							
8	64.5	38.1	51.2	60	41	50.5	.05		.05				
9	52.6	38.7	45.6	49	38	43.5	.09		.09		15:07	38	15:45
10	53.1	36.3	44.7	48	37	42.5							
11	57.7	34.9	46.3	49	35	42.0	.24	.5	.29				
12	54.1	34.4	44.2	44	32	38.0	T		T				
13	55.5	33.2	44.4	51	31	41.0	.03		.03		15:19	39	15:58
14	47.7	41.3	44.5	48	42	45.0	.38		.38				
15	50.1	38.4	44.3	46	37	41.5	.35		.35				
16	67.2	32.7	50.0	64	32	48.0							
17	80.2	33.9	57.1	84	42	63.0					15:30	40	16:10
18	69.2	44.8	57.0	64	54	59.0							
19	68.3	31.8	50.0	58	28	43.0	.08		.08				
20	56.5	41.5	49.0	58	42	50.0	.11		.11				
21	74.5	36.5	55.5	69	41	55.0					15:40	41	16:21
22	79.6	34.4	57.0	73	38	55.5							
23	85.3	38.1	61.7	76	43	59.5	T		T				
24	75.2	43.8	59.5	72	49	60.5	1.64		1.64				
25	51.3	37.9	44.1	36	31	33.5	T	T	T		15:50	42	16:32
26	53.2	33.7	43.4	47	30	38.5	.09	.1	.10				
27	59.4	37.2	48.3	54	35	44.5							
28	70.5	39.1	54.8	64	42	53.0	1.09		1.09				
29	66.4	50.1	58.2	63	49	56.0	.06		.06		15:59	42	16:41
30	69.4	42.5	55.9	68	45	56.5	.04		.04				
31	69.2	47.7	58.4	67	50	58.5	T		T				
TOTAL							4.25	3.6	4.61				
MEAN	62.0	36.9	49.4	58.0	37.2	47.6	.33	1.2	.45				

Five Day Mean

Week of	Sphagnum Max.	Sphagnum Min.	Sphagnum Mean	Air Max.	Air Min.	Air Mean
1-5	51.3	30.1	40.7	49.6	26.8	38.2
6-10	60.8	37.0	48.8	59.2	38.2	48.7
11-15	53.0	36.4	44.7	47.6	35.4	41.5
16-20	68.3	36.9	52.6	65.6	39.6	52.6
21-25	73.2	38.1	55.6	65.2	40.4	52.8
26-31	64.7	41.8	53.2	60.5	41.8	51.2

Monthly Temperature Extremes and Mean

	Sphag.	Air
High	85.3	84
Low	27.1	23
Mean	49.4	47.6

Wind

Mean Speed (MPH)	7.7
Prevailing Direction	E

Ppt.--Sum of rainfall and 1/10th of snowfall.

All temperatures in degrees F

T--Trace

Daylight--Interval between sunrise and sunset

Civil Twilight--Interval between sunrise and sunset and the time when the true position of the center of the sun is 6° below the horizon. First magnitude stars are just visible.

Total Light--Daylight and Civil Twilight.

METEOROLOGICAL SUMMARY

Month of June, 1970

Pinawa, Man. A.E.C.L. Site 50°15'N - 95°50'W

Daily Temperatures, Precipitation, Light, and Snow Depth

Day	Sphagnum Max.	Sphagnum Min.	Sphagnum Mean	Air Max.	Air Min.	Air Mean	Rain (In.)	Snow (in.)	Ppt. (in.)	Snow Depth (in.)	Daylight H. m.	Civil Twilight H. m.	Total Light H. m.
1	70.5	39.1	54.8	62	44	53.0					16:04	43	16:47
2	79.7	38.4	59.1	70	41	55.5							
3	82.5	35.8	59.1	79	42	60.5							
4	87.3	43.2	65.2	80	50	65.0							
5	89.7	40.3	65.0	86	44	65.0					16:11	43	16:54
6	87.1	50.0	68.6	82	64	68.0							
7	87.4	36.8	62.1	84	41	62.5							
8	92.8	43.0	67.9	89	61	75.0	.41		.41				
9	89.0	59.5	74.2	80	63	71.5					16:16	44	17:00
10	84.5	51.4	67.9	79	54	66.5							
11	67.9	59.1	63.5	65	57	61.0	.09		.09				
12	84.8	58.1	71.4	79	58	68.5							
13	84.1	54.8	69.4	80	58	69.0					16:20	44	17:04
14	82.4	50.7	66.6	77	52	64.5							
15	71.3	52.8	62.1	71	56	63.5	.02		.02				
16	71.0	50.7	60.9	72	56	64.0	.20		.20				
17	76.1	49.1	62.6	74	54	64.0	.03		.03		16:22	45	17:07
18	64.8	45.3	55.0	60	45	52.5							
19	79.5	36.5	58.0	69	35	52.0							
20	79.7	40.1	59.9	72	41	56.5							
21	79.5	41.1	60.3	72	50	61.0					16:23	45	17:08
22	87.3	41.0	64.1	81	41	61.0	.25		.25				
23	81.9	60.5	71.2	74	63	68.5	T		T				
24	77.4	43.6	60.5	67	43	55.0	.14		.14				
25	59.4	51.1	55.2	57	48	52.5	.01		.01		16:21	45	17:06
26	74.4	53.4	63.9	70	54	62.0							
27	72.3	46.5	59.4	72	48	60.0	.08		.08				
28	80.4	55.5	67.9	82	58	70.0	.01		.01				
29	90.8	60.0	75.4	86	65	75.5					16:20	45	17:03
30	80.2	58.5	69.3	84	65	74.5	.22		.22				
31													
TOTAL							1.46		1.46				
MEAN	79.9	48.2	64.0	75.2	51.6	89	.13		.13				

Five Day Mean

Week of	Sphagnum Max.	Sphagnum Min.	Sphagnum Mean	Air Max.	Air Min.	Air Mean
1-5	81.9	39.4	60.6	75.4	44.2	59.8
6-10	88.2	48.1	68.1	82.8	56.6	68.7
11-15	78.1	55.1	66.6	74.4	56.2	65.3
16-20	74.2	44.3	65.3	69.4	46.2	65.3
21-25	77.1	47.5	62.3	70.2	49.0	59.6
26-30	79.6	54.9	67.2	78.8	58.0	68.4

Monthly Temperature Extremes and Mean

	Sphag.	Air
High	90.8	89
Low	35.8	35
Mean	64.0	63.4

Wind

Mean Speed (MPH)	5.92
Prevailing Direction	SE

Ppt.--Sum of rainfall and 1/10th of snowfall.

All temperatures in degrees F

T--Trace

Daylight--Interval between sunrise and sunset

Civil Twilight--Interval between sunrise and sunset and the time when the true position of the center of the sun is 6° below the horizon. First magnitude stars are just visible.

Total Light--Daylight and Civil Twilight.

METEOROLOGICAL SUMMARY

Month of July, 1970

Pinawa, Man. A.E.C.L. Site 50°15'N - 95°50'W

Daily Temperatures, Precipitation, Light, and Snow Depth

Day	Sphagnum Max.	Sphagnum Min.	Sphagnum Mean	Air Max.	Air Min.	Air Mean	Rain (in.)	Snow (in.)	Ppt. (in.)	Snow Depth (in.)	Daylight H. m.	Civil Twilight H. m.	Total Light H. m.
1	86.5	51.4	69.0	80	55	67.5					16:18	44	17:02
2	78.5	58.1	68.3	70	60	65.0	.16		.16				
3	71.0	55.0	63.0	67	54	60.5	T		T				
4	81.3	40.3	60.8	73	48	60.5							
5	87.8	42.1	64.9	80	50	65.0	.22		.22		16:13	44	16:57
6	86.7	58.8	72.7	81	62	71.5							
7	82.0	53.6	67.8	75	59	67.0	T		T				
8	85.8	49.5	67.6	80	53	66.5							
9	92.5	51.4	71.9	89	61	75.0					16:08	43	16:51
10	93.9	61.6	77.8	88	65	76.5							
11	93.1	57.3	75.2	88	62	75.0	.34		.34				
12	84.1	65.6	74.8	84	67	75.5	.10		.10				
13	89.1	56.9	73.0	83	62	72.5	.40		.40		16:01	43	16:44
14	70.4	59.2	64.8	70	62	66.0	.95		.95				
15	84.4	51.4	67.9	81	55	68.0							
16	88.4	51.9	70.2	85	60	72.5							
17	80.7	55.8	68.2	72	56	64.0	T		T		15:53	42	16:35
18	61.5	57.2	59.3	62	57	59.5	.30		.30				
19	77.3	43.6	60.5	72	47	59.5							
20	83.2	42.9	63.0	75	44	59.5							
21	83.9	45.9	64.9	79	53	66.0					15:44	41	16:25
22	77.4	54.1	65.8	78	62	70.0	.22		.22				
23	78.9	61.1	70.0	82	62	72.0							
24	77.6	60.5	69.0	70	62	66.0	.38		.38				
25	88.8	53.3	71.0	84	55	69.5					15:34	40	16:17
26	84.0	66.1	75.0	81	67	74.0							
27	83.7	49.3	66.5	80	53	66.5							
28	89.4	50.5	69.9	85	53	69.0	.01		.01				
29	80.7	63.0	71.8	79	65	72.0	.55		.55		15:22	40	16:02
30	90.0	67.3	78.6	82	64	73.0							
31	72.5	57.8	65.2	68	60	64.0							
TOTAL							3.63		3.63				
MEAN	82.8	54.6	68.7	78.2	57.9	89	.33		.33				

Five Day Mean

Week of	Sphagnum Max.	Sphagnum Min.	Sphagnum Mean	Air Max.	Air Min.	Air Mean
1-5	81.0	49.4	65.2	74.0	53.4	63.7
6-10	88.2	55.0	71.6	82.6	57.0	71.3
11-15	84.2	58.1	71.1	81.2	61.6	71.4
16-20	78.2	54.3	64.2	73.2	52.8	63.0
21-25	81.3	55.0	68.1	78.6	58.8	68.7
26-31	83.4	59.0	71.7	79.2	60.3	69.8

Monthly Temperature Extremes and Mean

	Sphag.	Air
High	93.9	89
Low	42.1	44
Mean	68.7	68.1

Wind

Mean Speed (MPH)	5.45
Prevailing Direction	SSE

Ppt.--Sum of rainfall and 1/10th of snowfall.

All temperatures in degrees F

T--Trace

Daylight--Interval between sunrise and sunset

Civil Twilight--Interval between sunrise and sunset and the time when the true position of the center of the sun is 6° below the horizon. First magnitude stars are just visible.

Total Light--Daylight and Civil Twilight.

METEOROLOGICAL SUMMARY

Month of August, 1970

Pinawa, Man. A.E.C.L. Site 50°15'N - 95°50'W

Daily Temperatures, Precipitation, Light, and Snow Depth

	Sphagnum			Air			Rain (in.)	Snow (in.)	Ppt. (in.)	Snow Depth (in.)	Day-light H. m.	Civil Twilight H. m.	Total Light H. m.
Day	Max.	Min.	Mean	Max.	Min.	Mean							
1	83.7	46.9	65.3	83	53	68.0					15:14	39	15:53
2	66.9	47.6	57.2	64	52	58.0	.01		.01				
3	73.7	49.3	61.5	68	49	58.5							
4	75.2	43.6	59.4	78	51	64.5							
5	86.9	45.5	66.2	84	50	69.0	.03		.03		15:03	38	15:41
6	87.3	52.1	69.7	87	56	71.5							
7	89.9	61.6	75.8	88	65	76.5							
8	89.7	57.6	73.6	86	63	74.5							
9	79.0	62.1	70.5	78	63	70.5					14:50	37	15:27
10	85.3	47.8	66.6	82	45	63.5							
11	86.2	49.3	67.7	88	53	70.5							
12	88.1	55.2	71.7	89	58	73.5							
13	88.6	53.1	70.8	92	56	74.0					14:37	37	15:14
14	77.4	58.0	67.7	79	64	71.5							
15	69.5	48.3	58.9	65	53	59.0	.18		.18				
16	66.7	52.1	59.4	64	49	56.5							
17	78.5	44.5	61.5	84	49	66.5	.08		.08		14:23	36	14:59
18	73.6	62.1	67.8	75	64	69.5	.02		.02				
19	70.0	49.0	59.5	68	50	59.0							
20	67.7	46.4	57.1	68	48	58.0							
21	59.6	41.2	50.4	62	43	52.5	.56		.56		14:09	35	14:44
22	65.5	55.2	60.4	69	55	62.0							
23	74.6	40.5	57.6	76	41	58.5							
24	73.6	41.2	57.4	77	41	59.0							
25	73.5	44.8	59.1	70	47	58.5					13:55	34	14:29
26	74.5	42.4	58.4	78	43	60.5	.14		.14				
27	66.5	41.1	53.8	69	57	62.5							
28	68.2	39.8	54.0	70	40	55.0	.08		.08				
29	68.3	47.2	57.7	70	50	60.0	1.29		1.29		13:41	34	14:15
30	64.1	45.4	54.7	64	46	55.0							
31	66.1	36.7	51.4	69	36	52.5							
TOTAL							2.39		2.39				
MEAN	74.5	49.0	62.0	92	36	63.5	.27		.27				

Five Day Mean

Week of	Sphagnum			Air		
	Max.	Min.	Mean	Max.	Min.	Mean
1-5	77.3	46.6	61.9	75.4	51.0	62.2
6-10	86.2	56.2	71.2	84.2	58.4	71.3
11-15	82.0	52.8	67.4	82.6	56.8	69.7
16-20	71.3	50.8	61.1	71.8	52.0	61.9
21-25	69.4	44.6	57.0	70.8	45.4	58.1
26-31	68.0	44.2	55.0	70.0	45.3	57.6

Monthly Temperature Extremes and Mean

	Sphag.	Air
High	89.9	92
Low	36.7	36
Mean	62.0	63.5

Wind

Mean Speed (MPH)	5.23
Prevailing Direction	SSE

Ppt.--Sum of rainfall and 1/10th of snowfall.

All temperatures in degrees F

T--Trace

Daylight--Interval between sunrise and sunset

Civil Twilight--Interval between sunrise and sunset and the time when the true position of the center of the sun is 6° below the horizon. First magnitude stars are just visible.

Total Light--Daylight and Civil Twilight.

METEOROLOGICAL SUMMARY

Month of September, 19 70

Pinawa, Man. A.E.C.L. Site 50°15'N - 95°50'W

Daily Temperatures, Precipitation, Light, and Snow Depth

	Sphagnum			Air			Rain (in.)	Snow (in.)	Ppt. (in.)	Snow Depth (in.)	Day-light H. m.	Civil Twilight H. m.	Total Light H. m.
Day	Max.	Min.	Mean	Max.	Min.	Mean							
1	74.8	42.1	58.4	80	46	63.0	.05		.05		13:31	34	14:15
2	74.9	62.1	68.5	72	64	68.0	.01		.01				
3	73.1	63.8	68.4	74	64	69.0	T		T				
4	71.2	53.8	62.5	72	55	63.5							
5	78.4	51.9	65.1	85	54	69.5					13:16	33	13:49
6	80.3	65.8	73.0	84	68	76.0	.01		.01				
7	64.5	51.0	57.7	64	56	60.0	.41		.41				
8	61.8	52.6	52.2	62	44	53.0	.32		.32				
9	57.1	50.3	53.7	57	51	54.0	.02		.02		13:01	33	13:34
10	58.2	40.7	49.4	58	39	48.5							
11	53.2	36.7	44.9	53	37	45.0	.61		.61				
12	50.8	40.3	45.5	48	38	43.0	.08		.08				
13	48.7	35.1	41.9	45	31	38.0					12:47	33	13:20
14	53.5	33.9	43.7	54	29	41.5	.01		.01				
15	48.9	37.0	42.9	46	36	41.0	.33		.33				
16	60.7	34.4	47.5	68	34	51.0							
17	63.1	41.5	52.3	65	48	56.5					12:32	32	13:04
18	66.6	41.0	53.8	74	44	59.0							
19	73.9	42.2	58.0	82	47	64.5							
20	73.3	50.0	61.6	73	53	63.0	1.08		1.08				
21	61.4	48.5	55.0	62	53	57.5	.18		.18		12:17	32	12:49
22	50.5	44.2	47.3	48	41	44.5	T		T				
23	60.1	37.4	48.7	69	36	52.5							
24	58.4	46.7	52.6	64	48	56.0	.19		.19				
25	55.0	46.2	50.6	53	43	48.0							
26	51.0	40.8	45.9	50	38	44.0	T		T				
27	49.2	34.6	41.9	52	30	41.0							
28	55.6	33.9	44.8	63	30	46.5							
29	60.2	41.0	50.6	69	47	58.0					11:47	32	12:19
30	64.9	35.3	50.1	76	35	55.5							
31													
TOTAL							3.3		3.3				
MEAN	61.8	44.6	52.0	85	29	54.4	.25		.25				

Five Day Mean

Week of	Sphagnum			Air		
	Max.	Min.	Mean	Max.	Min.	Mean
1-5	74.5	54.7	64.6	76.6	56.6	66.6
6-10	64.4	52.1	57.2	65.0	51.6	58.3
11-15	51.0	36.6	43.8	49.2	34.2	41.7
16-20	67.5	41.8	54.6	72.4	45.2	58.8
21-25	57.1	44.6	50.8	59.2	44.2	51.7
26-30	56.2	37.1	46.7	62.0	36.0	49.0

Monthly Temperature Extremes and Mean

	Sphag.	Air
High	80.3	85
Low	33.9	29
Mean	52.0	54.4

Wind

Mean Speed (MPH)	5.54
Prevailing Direction	SSE

Ppt.--Sum of rainfall and 1/10th of snowfall.

All temperatures in degrees F

T--Trace

Daylight--Interval between sunrise and sunset

Civil Twilight--Interval between sunrise and sunset and the time when the true position of the center of the sun is 6° below the horizon. First magnitude stars are just visible.

Total Light--Daylight and Civil Twilight.

METEOROLOGICAL SUMMARY

Month of October, 1970

Pinawa, Man. A.E.C.L. Site 50°15'N - 95°50'W

Daily Temperatures, Precipitation, Light, and Snow Depth

Day	Sphagnum Max.	Sphagnum Min.	Sphagnum Mean	Air Max.	Air Min.	Air Mean	Rain (in.)	Snow (in.)	Ppt. (in.)	Snow Depth (in.)	Daylight H. m.	Civil Twilight H. m.	Total Light H. m.
1	57.5	42.4	50.0	65	51	58.0	T		T		11:39	32	12:11
2	46.0	41.2	43.6	47	40	43.5	.21	2.0	.41				
3	46.8	35.3	41.0	51	33	42.0							
4	53.5	37.5	45.5	63	38	50.5							
5	65.5	40.9	53.2	71	47	59.0					11:24	32	11:56
6	62.6	38.1	50.4	67	42	54.5	.05		.05				
7	42.9	36.7	39.8	40	33	36.5							
8	42.0	35.1	38.5	38	33	33.5		.1	.01				
9	35.1	33.9	34.5	31	29	30.0		5.5	.55		11:10	32	11:42
10	34.6	33.4	34.0	36	24	30.0							
11	34.1	32.8	33.4	40	22	31.0							
12	35.9	33.7	34.8	51	33	42.0							
13	37.5	33.7	35.6	40	30	35.0					10:56	32	11:28
14	34.6	32.5	33.6	39	28	33.5							
15	36.3	30.1	33.2	51	22	36.5							
16	40.0	30.8	35.4	61	30	45.5							
17	69.7	32.0	50.8	57	30	43.5					10:40	33	11:13
18	64.9	26.8	45.8	53	25	39.0							
19													
20													
21													
22													
23													
24													
25													
26													
27													
28													
29													
30													
31													
TOTAL													
MEAN													

Five Day Mean

Week of	Sphagnum Max.	Sphagnum Min.	Sphagnum Mean	Air Max.	Air Min.	Air Mean
1-5	53.9	39.5	44.7	59.4	41.8	50.6
6-10	43.4	35.4	39.4	42.4	32.2	36.9
11-15	35.7	32.6	34.1	44.2	27.0	35.6
16-20	59.2	29.9	44.0	57.0	28.3	42.7

Monthly Temperature Extremes and Mean

	Sphag.	Air
High		
Low		
Mean		

Wind

Mean Speed (MPH)	
Prevailing Direction	

Ppt.--Sum of rainfall and 1/10th of snowfall.

All temperatures in degrees F

T--Trace

Daylight--Interval between sunrise and sunset

Civil Twilight--Interval between sunrise and sunset and the time when the true position of the center of the sun is 6° below the horizon. First magnitude stars are just visible.

Total Light--Daylight and Civil Twilight.

APPENDIX C

List of plant species and numbers per 1 meter quadrat sample, Pinawa Bog, October 1969

Species	Number of plants/species/1 meter quadrat																				Total	No. of quadrat species occurred in
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20		
Chamaedaphne calyculata	207	80	-	30	-	-	63	69	141	67	83	105	36	-	48	93	37	86	75	163	1383	16
Ledum groenlandicum	-	73	15	67	6	40	17	94	-	-	-	-	76	-	80	-	91	63	46	-	668	12
Kalmia polifolia	32	37	-	-	8	-	3	11	2	-	4	9	-	-	4	4	8	-	3	9	134	13
Vaccinium oxycoccus	64	200	500+	100	249	157	343	238	500+	500+	147	176	414	500+	500+	175	500+	340	470	500+	7573	20
Betula glandulosa	7	5	-	-	1	3	-	1	-	-	-	2	-	-	6	4	-	-	1	-	84	9
Maianthemum canadense	185	150	-	70	60	34	91	55	23	61	48	74	56	-	87	68	42	-	-	56	1160	16
Eriophorum angustifolium	-	-	-	40	-	-	-	-	37	-	1	-	20	-	-	-	30	-	20	-	148	6
Larix laricina	-	-	-	-	1	1	-	-	-	-	1	1	-	-	-	1	2	-	-	1	8	7
Picea mariana	-	1	-	6	-	-	-	-	-	1	-	-	-	-	1	-	3	-	-	-	51	14
P. mariana (seedlings)	-	-	-	8	1	11	-	3	-	1	-	-	2	-	-	-	4	-	7	2		
Sarracenia purpurea	8	1	11	-	7	1	-	8	6	12	-	2	5	9	-	-	3	5	7	-	85	14
Andromeda polifolia	8	60	35	-	40	9	11	-	92	6	35	23	-	13	41	27	6	-	-	31	437	15
Carex spp.	14	15	18	-	4	28	70	6	-	8	3	7	-	17	11	-	-	31	18	14	264	15

N.B. Where *Vaccinium oxycoccus* occurred in numbers greater than 500, no further counts were made and is noted as 500+.

Picea mariana and *P. mariana* seedlings were grouped together.

APPENDIX D

Recorded Northern and Western Collections of *Sarracenia purpurea* L.

Code No.	Site	Reference
1	North West River, Labrador	National Museum of Canada
2	Goose Bay, Labrador	University of Wyoming, Department of Botany
3	Indian Harbor, Labrador	Université Laval Herbier Louis-Marie (Ph.D. Thesis - Mr. C. Rousseau Personal Correspondence L. Cinq-Mars)
4	Ashuanipi Lake, Labrador	National Museum of Canada
5	Mistassini Lake, Quebec	Université Laval Herbier Louis-Marie (Ph.D. Thesis - Mr. C. Rousseau Personal Correspondence L. Cinq-Mars)
6	Mistassini Lake, Quebec	*Ibid.*
7	Vicinity of Churchill Falls, Labrador	*Ibid.*
8	Vicinity of Fort Rupert, Quebec	*Ibid.*
9	Vicinity of Fort George, Quebec	*Ibid.*
10	"Rock End" Trail - Smokey Falls near Kapuskasing, Cochrane District, Ontario	University of Toronto Herbaria
11	Lake Allawapiskat, Ontario	*Ibid.*

APPENDIX D (continued)

Code No.	Site	Reference
12	Fawn River, near Mink Creek, Ontario	University of Guelph (Ph.D. Thesis - D.R. Moir, 1958 A Floristic survey of the Severn River Drainage of Northwestern Ontario. University of Minnesota. University Microfilm, Ann Arbor, Michigan)
13	Big Trout Lake, Ontario	*Ibid.*
14	Sandy Lake, Ontario	*Ibid.*
15	Near Senia Lake, Ontario	*Ibid.* University of Toronto
16	Amery, on Nelson River, Manitoba	National Museum of Canada
17	West of Oxford House, Manitoba	University of Manitoba Herbaria
18	Aweme, Manitoba Treesbank, Manitoba	Canada Department of Agriculture, Ottawa National Museum of Canada
19	Windrum Lake, Saskatchewan	National Museum of Canada
20	Cree Lake, Saskatchewan	Canada Department of Agriculture, Ottawa National Museum of Canada University of Saskatchewan
21	Lake Athabaska, Northwest Territories	National Museum of Canada University of Saskatchewan Canada Department of Agriculture, Ottawa Harvard University, Gray Herbaria
22	Fort McMurray, Alberta	Canada Department of Agriculture, Ottawa

APPENDIX D (continued)

Code No.	Site	Reference
23	Great Bear Lake, Northwest Territories	Scoggan, H.J. (1957) Flora of Manitoba. p328 National Museum of Canada Bulletin, No. 140
24	Doré Lake, Saskatchewan	Canada Department of Agriculture, Ottawa
25	Big Sandy Lake, Saskatchewan	Canada Department of Agriculture, Ottawa University of Saskatchewan
26	Flin Flon, Manitoba	National Museum of Canada
27	Nipawin Lake, Saskatchewan	Museum of Natural History Province of Saskatchewan, Regina
28	Prince Albert, Saskatchewan	University of Saskatchewan University of Manitoba Herbaria National Museum of Canada
29	Edson, Alberta	Moss, E.H. (1967) Flora of Alberta. University of Toronto Press. pp268-269

APPENDIX E - TABLE I

Results of ^{137}Cesium uptake by *Wyeomyia smithii* 3rd instar larvae when fed ^{137}Cs labeled dog food at 18L:6D/27°C

Diapause 3rd Instar (Field reared - held at 12L:12D/20°C)			Non-diapause 3rd Instar (Laboratory reared - 18L:6D/27°C)		
Time (Hrs.) after start	n	cpm Mean ± S.D.	Time (Hrs.) after start	n	cpm Mean ± S.D.
1	20	16.8±3.07	1	20	29.8±6.3
3	20	16.7±1.9	3	20	37.4±6.8
6	20	17.8±5.8	6	20	39.9±10.0
12	20	17.7±2.6	12	20	37.5±11.1
24	20	17.2±1.6	24	20	32.8±6.7

APPENDIX E - Table 2

Results of ^{137}Cesium uptake by *Wyeomyia smithii* 3rd instar larvae reared in a nutrient-free ^{137}Cs media at 18L:6D/27°C

Diapause 3rd Instar (Field reared - held at 12L:12D/20°C)			Non-diapause 3rd Instar (Laboratory reared - 18L:6D/27°C)		
Time (Hrs.) after start	n	cpm Mean ± S.D.	Time (Hrs.) after start	n	cpm Mean ± S.D.
3	10	14.12±1.40	3	10	24.04±11.41
6	10	15.79±2.09	6	10	32.43±12.97
12	10	17.93±3.80	12	10	40.69±27.94
24	10	22.81±9.23	24	10	33.67±13.21
48	8	31.58±15.73	48	9	34.45±16.25

APPENDIX F

Individual freezing points for six different larval groups of *W. smithii*

No.	Diapause 3rd held at 12L/20°C (D3)	Non-Diapause 3rd reared at 18L/27°C (ND3)	Diapause 3rd field coll. 29/12/70 (D3F)	Diapause 3rd treated 1 month at 20°C 2 months at 10°C 1 month at 5°C 12L:12D (D3H)	2nd Instar reared at 18L/27°C (II)	4th Instar reared at 18L/27°C (IV)
1	-1.5	0	-2.5	-2.0	-12.0	0
2	-1.0	0	0	-6.0	-10.0	-6.5
3	-9.5	-6.0	-10.0	0	-11.5	-5.5
4	-2.0	0	-1.5	-2.0	-4.0	0
5	-2.0	-8.5	-4.0	-5.0	-1.5	-1.5
6	0	-8.0	-3.5	-6.5	-14.5	-3.5
7	-11.0	0	0	0	-3.5	-3.5
8	-13.5	-4.5	0	0	-7.5	0
9	-10.5	-0.5	-2.5	-2.5	-13.5	0
10	-1.0	-1.5	-4.0	0	-5.5	-2.5
11	-10.0	-8.5	-1.5	0	-13.5	0
12	-11.5	0	-2.5	-6.0	-11.0	0
13	-12.5	-6.5	-7.5	-4.5	-4.0	-2.0
14	-10.5	0	-1.5	-2.5	-6.0	-8.0
15	-4.5	0	-1.0	-3.0	-7.5	-0.5

APPENDIX F (continued)

No.	Diapause 3rd held at 12L/20°C (D3)	Non-Diapause 3rd reared at 18L/27°C (ND3)	Diapause 3rd field coll. 29/12/70 (D3F)	Diapause 3rd treated 1 month at 20°C 2 months at 10°C 1 month at 5°C 12L:12D (D3H)	2nd Instar reared at 18L/27°C (II)	4th Instar reared at 18L/27°C (IV)
16	0	-5.5	-3.5	-6.5	-9.0	-7.5
17	0	0	-4.5	0	-14.5	0
18	-14.5	-2.5	-1.0	-5.0	-11.0	-3.0
19	-7.0	-5.0	-5.0	-7.5	-3.5	0
20	-11.5	-8.5	-3.0	-8.0	-3.0	0
21	-5.0	-2.5	-0.5	0	-4.5	0
22	-8.5	0	-3.5	-6.0	-6.0	-4.5
23	0	-3.5	-7.5	-6.0	-16.0	0
24	-11.5	-3.0	-1.5	-5.0	-7.0	0
25	0	-8.5	-4.5	-4.0	-12.0	-5.0
26	-1.0	-10.5	-6.0	-7.5	-15.0	-3.5
27	-2.0	-11.0	-12.0	-4.5	-8.5	0
28	-8.0	-10.5	-0.5	-12.0	-12.0	-3.0
29	-7.0	-1.5	-1.5	-7.5	-11.0	-3.5
30	-7.5	-2.5	-0.5	-10.5	-9.5	0

APPENDIX F (continued)

No.	Diapause 3rd held at 12L/20°C (D3)	Non-Diapause 3rd reared at 18L/27°C (ND3)	Diapause 3rd field coll. 29/12/70 (D3F)	Diapause 3rd treated 1 month at 20°C 2 months at 10°C 1 month at 5°C 12L:12D (D3H)	2nd Instar reared at 18L/27°C (II)	4th Instar reared at 18L/27°C (IV)
31	-7.5	-6.5	-4.5	-7.0	-8.0	0
32	-4.5	-3.5	-7.0	-5.0	-8.5	-3.0
33	0	-9.0	-1.5	-11.0	-6.5	0
34	0	-0.5	-3.5	-3.0	-11.5	0
35	-5.0	0	-0.5	-7.5	-14.0	0
36	0	0	-11.0	-5.0	-10.0	0
37	-11.0	-4.0	-6.5	-7.5	-12.0	0
38	-4.0	-0.5	-1.0	-2.5	-5.0	-0.5
39	-4.5	-5.0	0	-4.5	-9.5	-11.0
40	-8.5	-3.5	-1.0	-4.5	-12.5	0
41	0	-5.5	-3.5	-7.0	-7.5	0
42	-2.0	0	-1.0	-8.0		0
43	-11.0	-6.5	0	-8.0		-9.0
44	-5.5	-0.5	-5.5	-11.5		0
45	-3.0	0	-3.0	-2.0		-2.5

APPENDIX F (continued)

No.	Diapause 3rd held at 12L/20°C (D3)	Non-Diapause 3rd reared at 18L/27°C (ND3)	Diapause 3rd field coll. 29/12/70 (D3F)	Diapause 3rd treated 1 month at 20°C 2 months at 10°C 1 month at 5°C 12L:12D (D3H)	2nd Instar reared at 18L/27°C (II)	4th Instar reared at 18L/27°C (IV)
46	-4.5	-6.0	-4.0	-3.0		0
47	-6.0	-3.0	-12.0	-6.5		-1.0
48	-7.5	0	0	-7.5		0
49	-3.5	0	-4.0	-6.5		0
50	-9.0	0	-3.5	-6.5		0
Mean ± one standard deviation	5.45±4.38	3.46±3.50	3.40±3.13	4.99±3.16	9.10±3.79	1.81±2.76

Figure 1. Location of study areas. (1) Kenora, (2) Pinawa, (3) Telford, (4) The Pas. Actual collecting site shown by ★

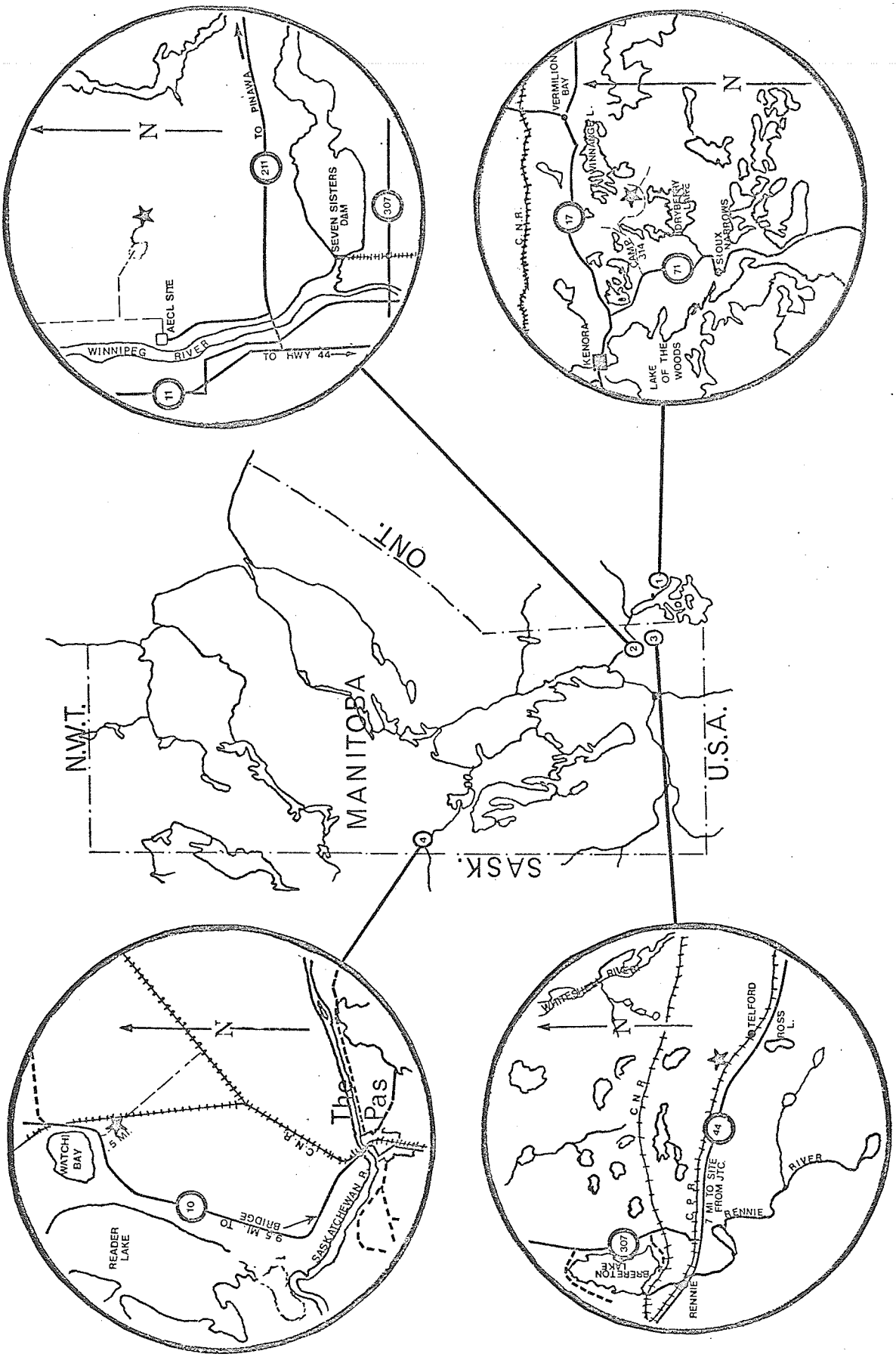

N
TO PINAWA
211
SEVEN SISTERS DAM
307
AECL SITE
WINNIPEG RIVER
TO HWY 44
11
N
VERMILION BAY
WINNANGE L.
C.N.R.
17
CAMP 314
DRYBERRY LAKE
71
SIOUX NARROWS
KENORA
LAKE OF THE WOODS
ONT.
N.W.T.
MANITOBA
SASK.
U.S.A.
1
2
3
4
N
WATCHI BAY
5 MI
C.N.R.
The Pas
10
9.5 MI TO BRIDGE
SASKATCHEWAN R.
READER LAKE
N
WINNIPEG RIVER
TELFORD
ROSS L.
C.N.R.
44
C.P.R.
7 MI TO SITE FROM JTC
RENNIE
RIVER
307
BRERETON LAKE
RENNIE

Figure 1

Figure 2. Vegetation on map of Pinawa Bog and Study Area No. 2.

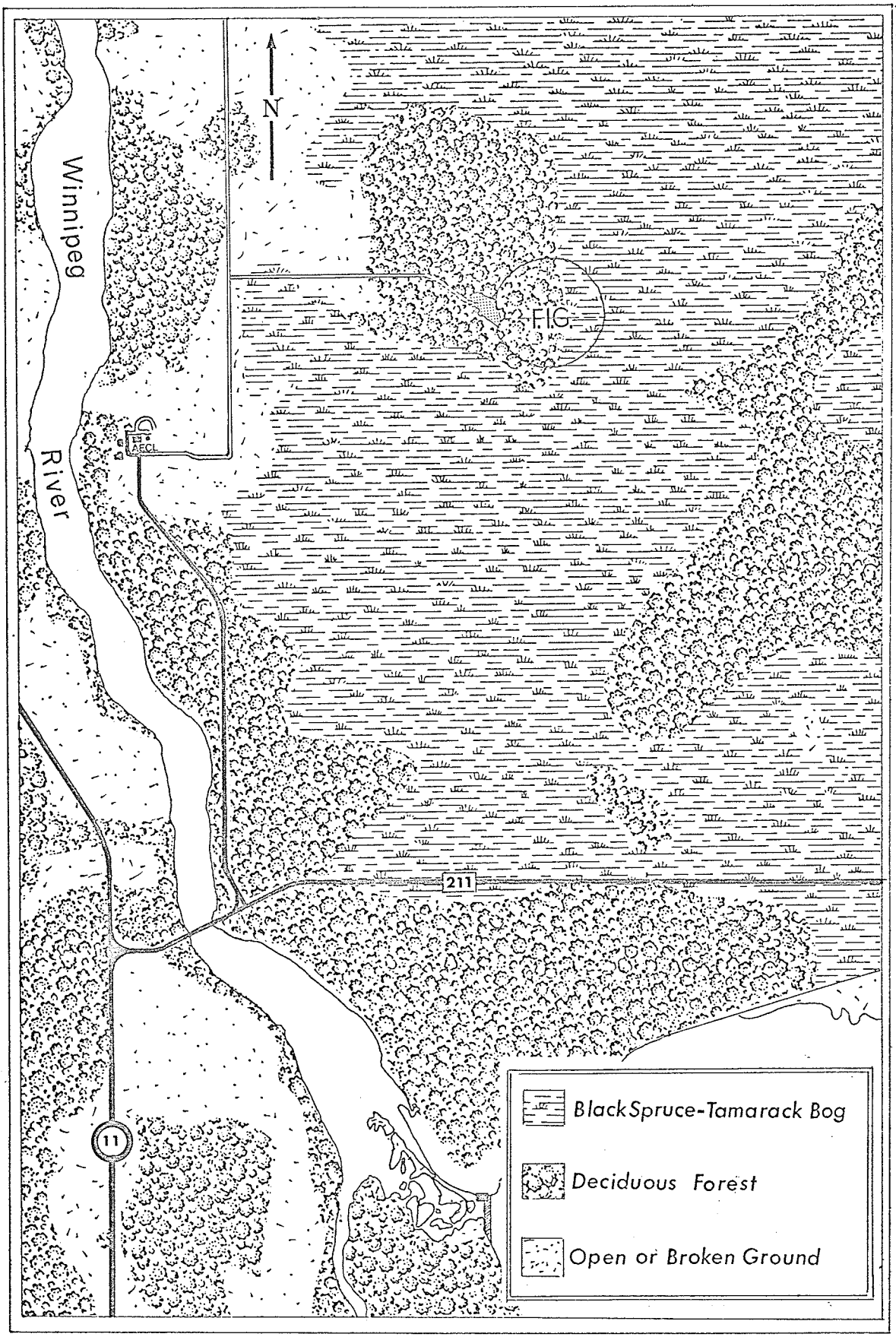

N
Winnipeg
River
FIG.
AECL
211
11
Black Spruce-Tamarack Bog
Deciduous Forest
Open or Broken Ground

Figure 2

Figure 3. Aerial view of the FIG area located in the Pinawa Bog.

Figure 3

Figure 4. Taylor Temperature Recorder, Pinawa Bog.

Figure 5. Location of Temperature probe for recording of sphagnum temperatures, Pinawa Bog.

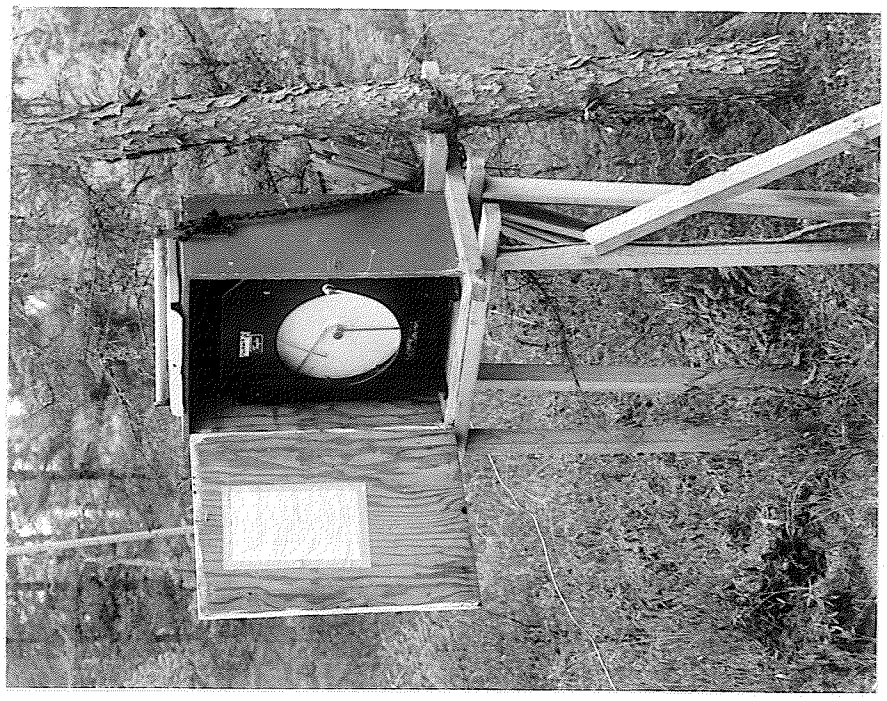


Figure 4

Figure 5

Figure 6. Glass vials used for artificial pitchers

A. 23 mm. opening

B. 16 mm. opening

C. 12 mm. opening

Figure 7. Artificial pitchers in the field, Telford Bog.

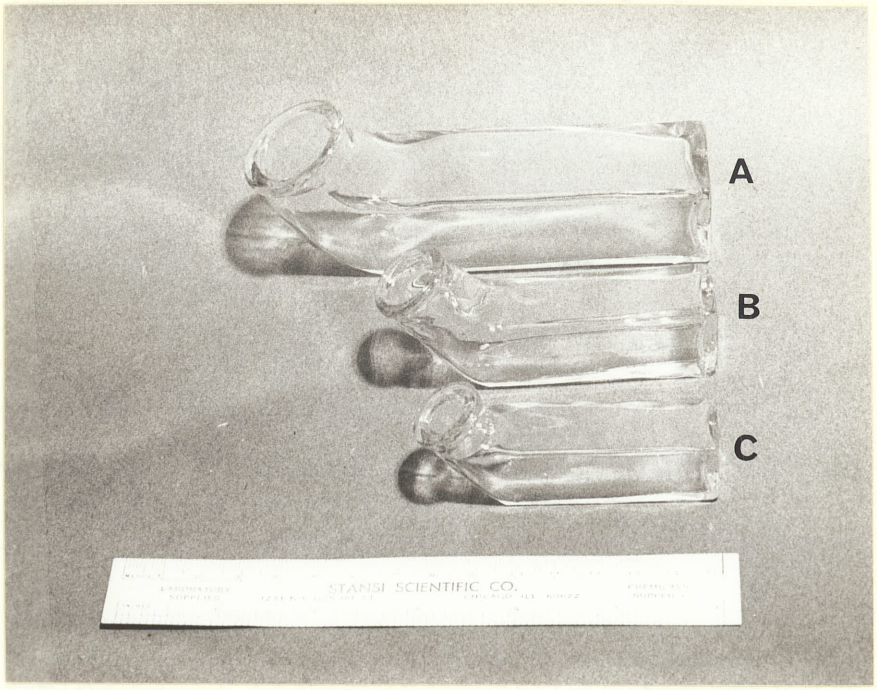


Figure 6

Figure 7

Figure 8. Adult emergence cage used in laboratory rearing of *Wyeomyia smithii*.

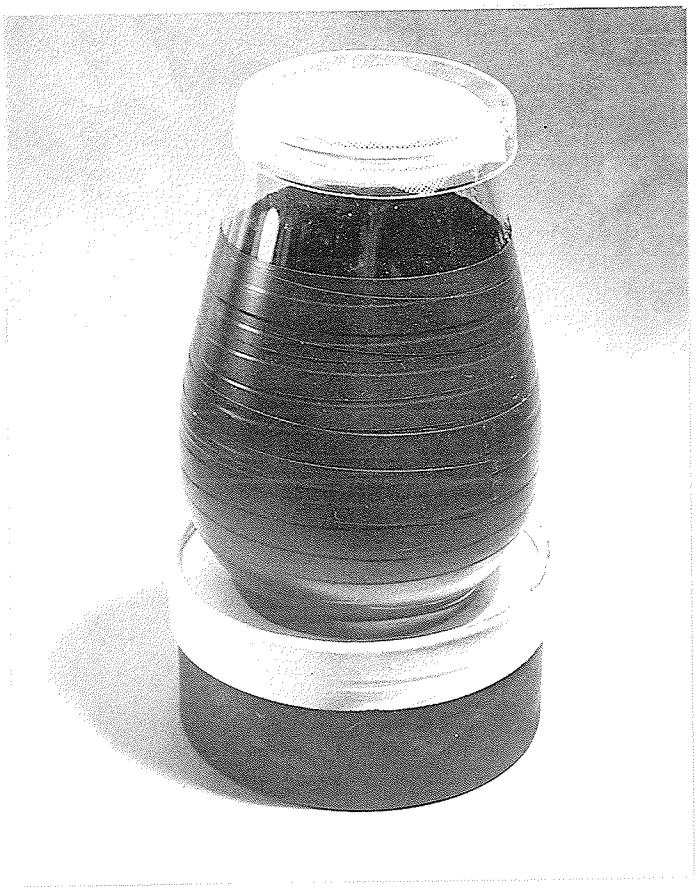
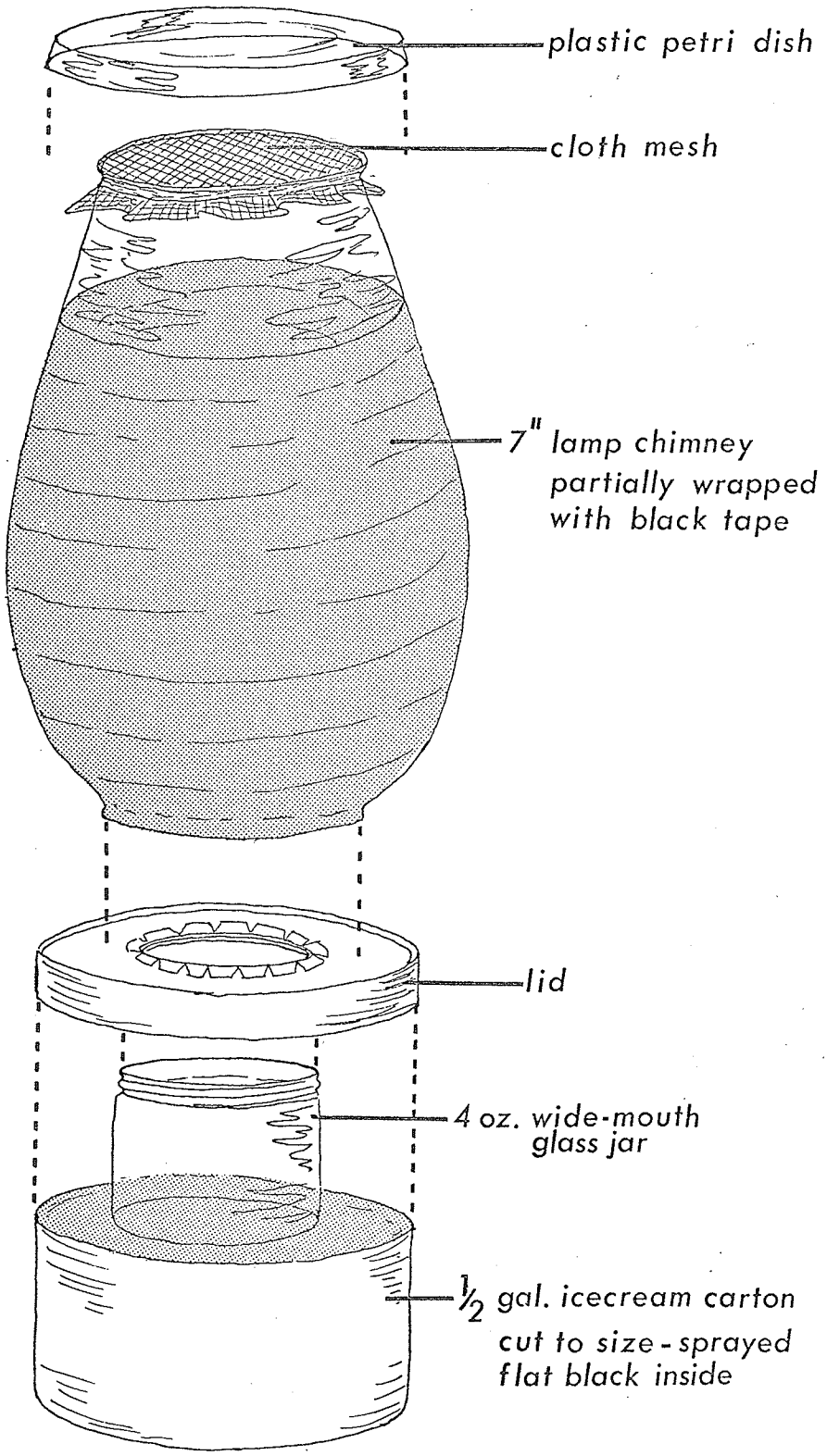


Figure 8

Figure 9. Breakaway view of adult emergence cage, illustrating construction methods.



Adult Emergence Cage – W. smithii

Figure 9

Figure 10. B.O.D. incubator used in laboratory rearing of *Wyeomyia smithii*. Upper shelf contains adult emergence cages. Lower shelves contain larval rearing pans. Foil on the door aids reflection of light.

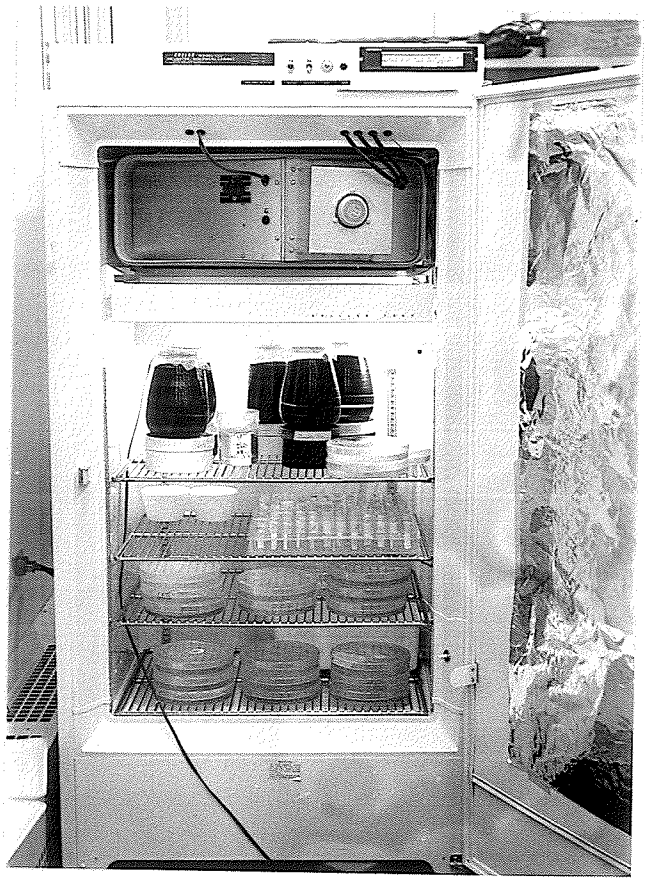


Figure 10

Figure 11. Water bath used in diapause induction experiments.

Figure 12. Top view of water bath, illustrating method of sectioning.

Figure 13. Light apparatus for water bath.

Figure 11

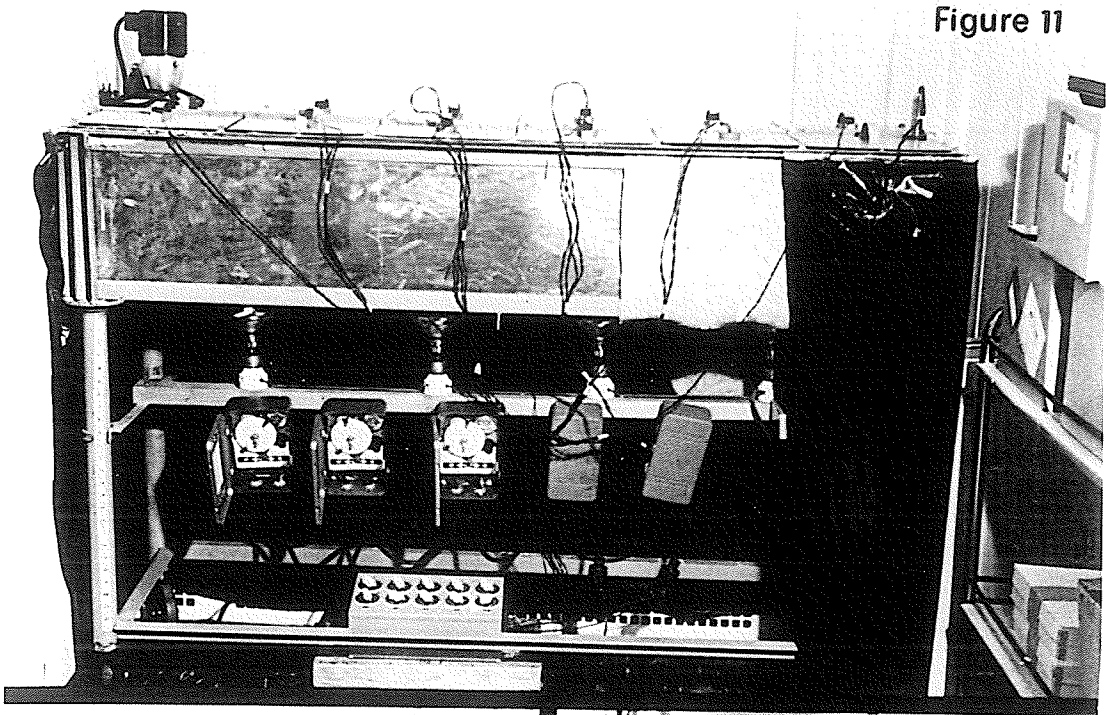


Figure 12

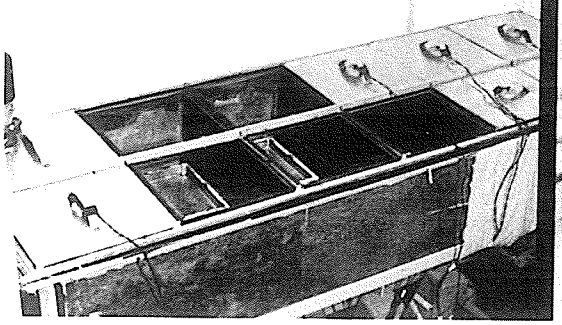


Figure 13

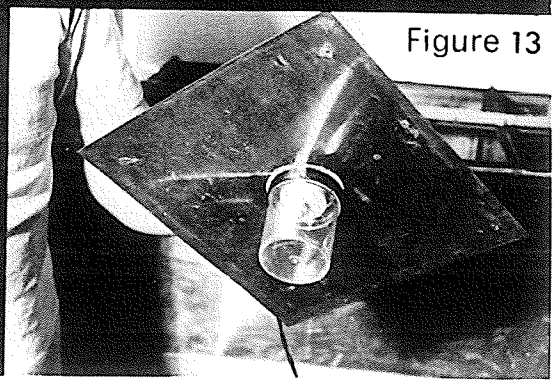


Figure 14. Diagram of cooling bath showing the thermocouple, air chambers, (A1, A2, A3) coolant, and thermos.

Figure 15. Experimental apparatus used in supercooling experiments A--recording potentiometer; B--thermocouple and air chamber; C--insulated wide mouth thermos.

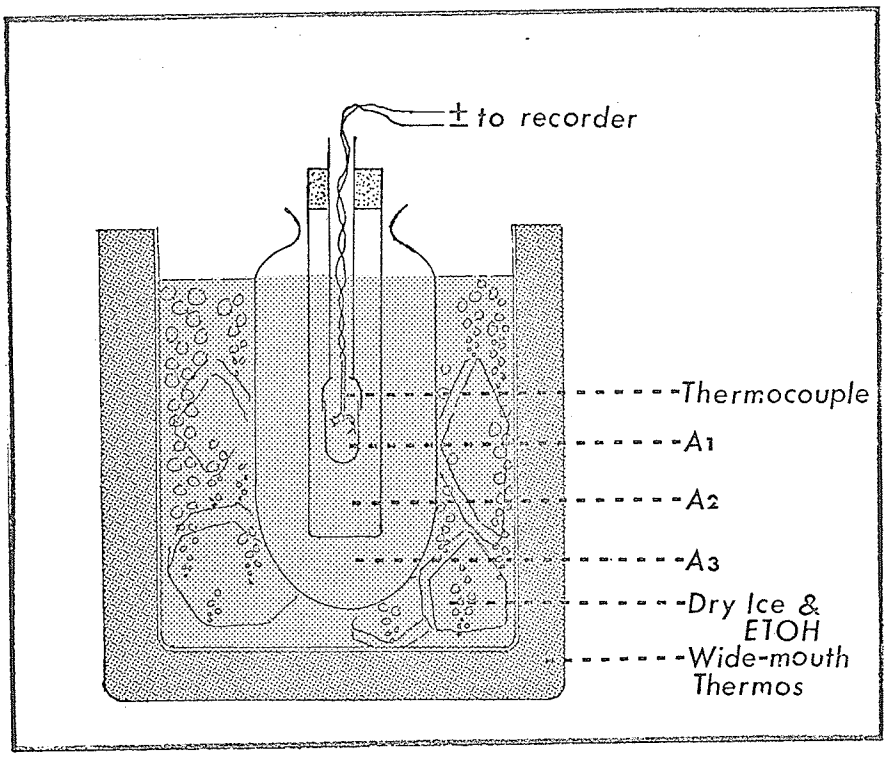


Figure 14

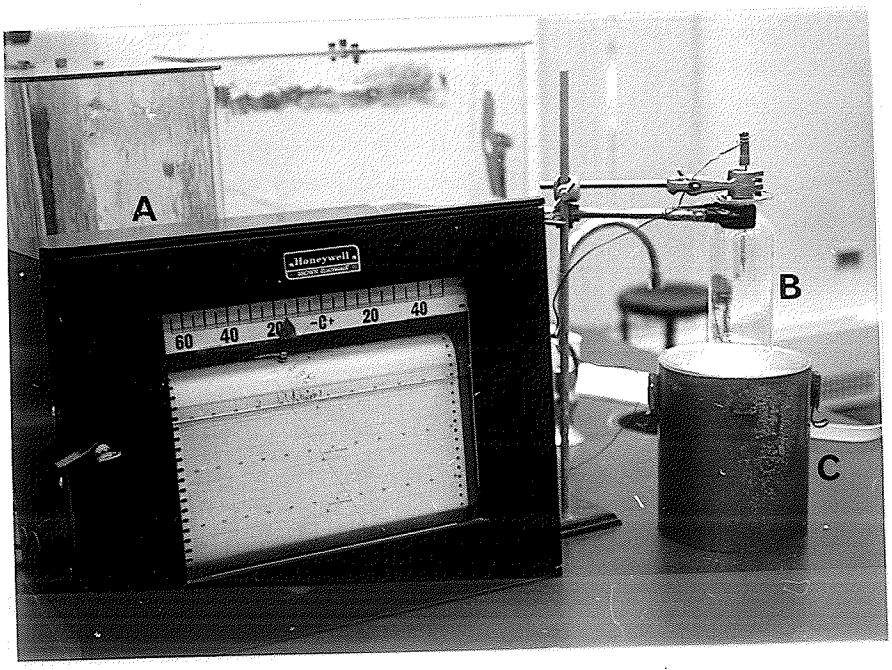


Figure 15

Figure 16. *Sarracenia purpurea* L. as it occurs in its natural habitat.

Figure 17. Whole leaf of *Sarracenia purpurea* L.

Figure 16

Figure 17

Figure 18. Cross section of a *Sarracenia purpurea* leaf revealing the five zones: (1) flap-like appendage bearing spines and nectar glands; (2) slick, ridged zone which also contains nectar glands; (3) smooth, waxed zone; (4) absorption zone containing hairs and absorbing cells; (5) small, smooth zone devoid of hairs or spines, the function of which is unknown.

Figure 19. Flower of *Sarracenia purpurea* L.

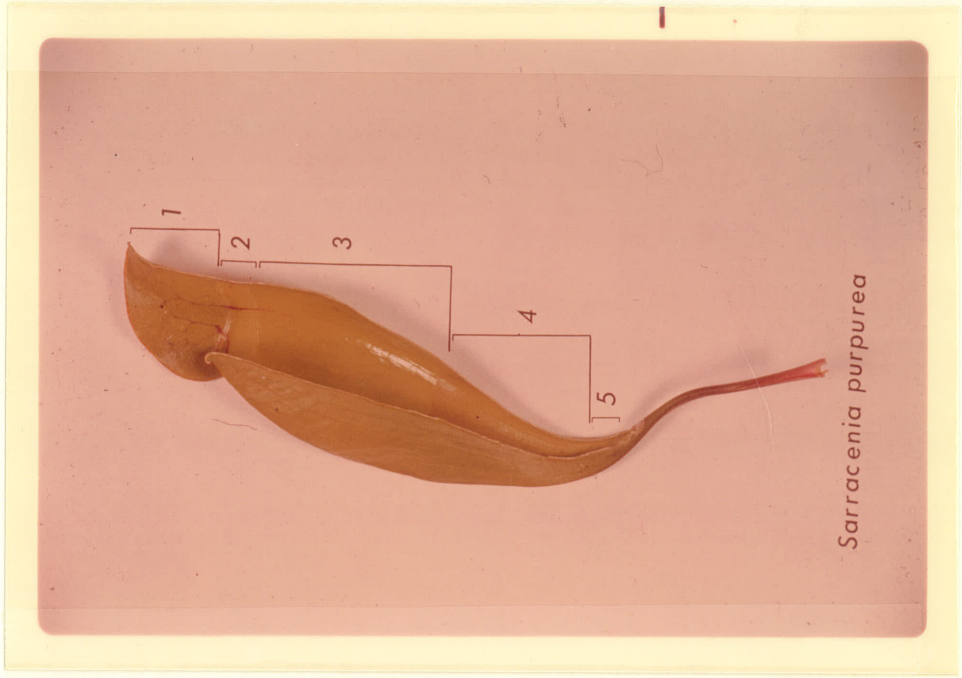


Figure 18

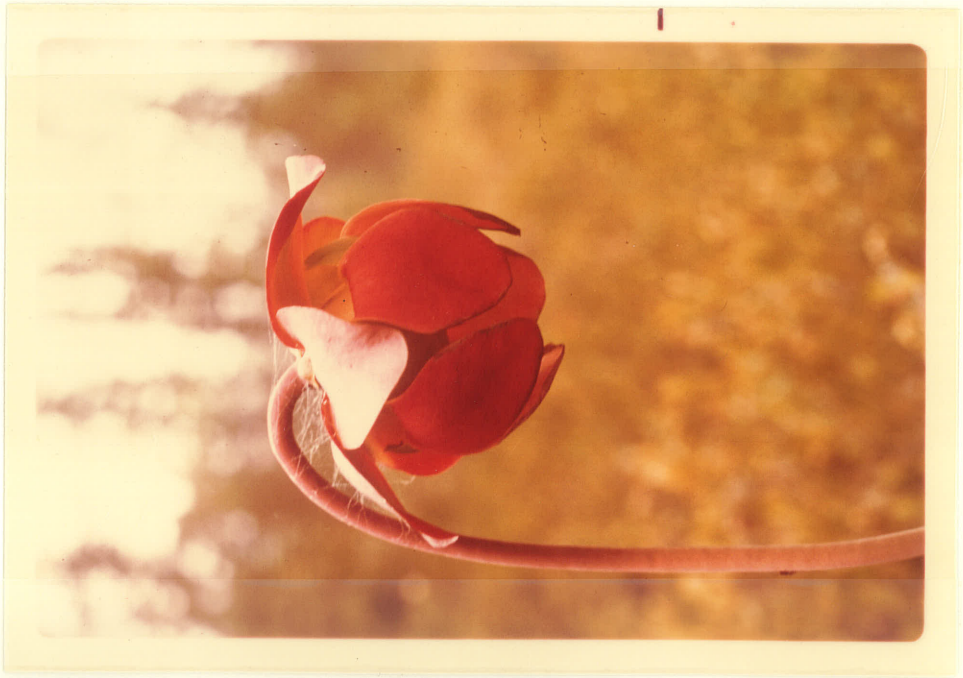


Figure 19

Figure 20. Stalks and flower of *Sarracenia purpurea* arising from a rosette of leaves.

Figure 20

Figure 21. Fibrous root system of *Sarracenia purpurea*.

Figure 22. Overwintered leaves in The Pas Bog.

Figure 21

Figure 22

Figure 23. Decay beginning in the leaf of *Sarracenia purpurea* L. With time the decay process will continue downward toward the basal portion of the leaf.

Figure 24. An almost completely decayed leaf.

Figure 23

Figure 24

Figure 25. Young leaves (see arrow) begin their growth in the spring. Large, dark-veined leaves are from previous year's growth.

Figure 26. Newly opened leaves of *Sarracenia purpurea* L., Young leaves are a soft, pale green but eventually darken (see leaf in background) with maturity.

Figure 25

Figure 26

Figure 27. Flower buds as they first appear in the spring.

Figure 28. A fully mature flower may attain a height of 18 inches and is conspicuous above the surrounding vegetation of the bogs.

Figure 27

Figure 28

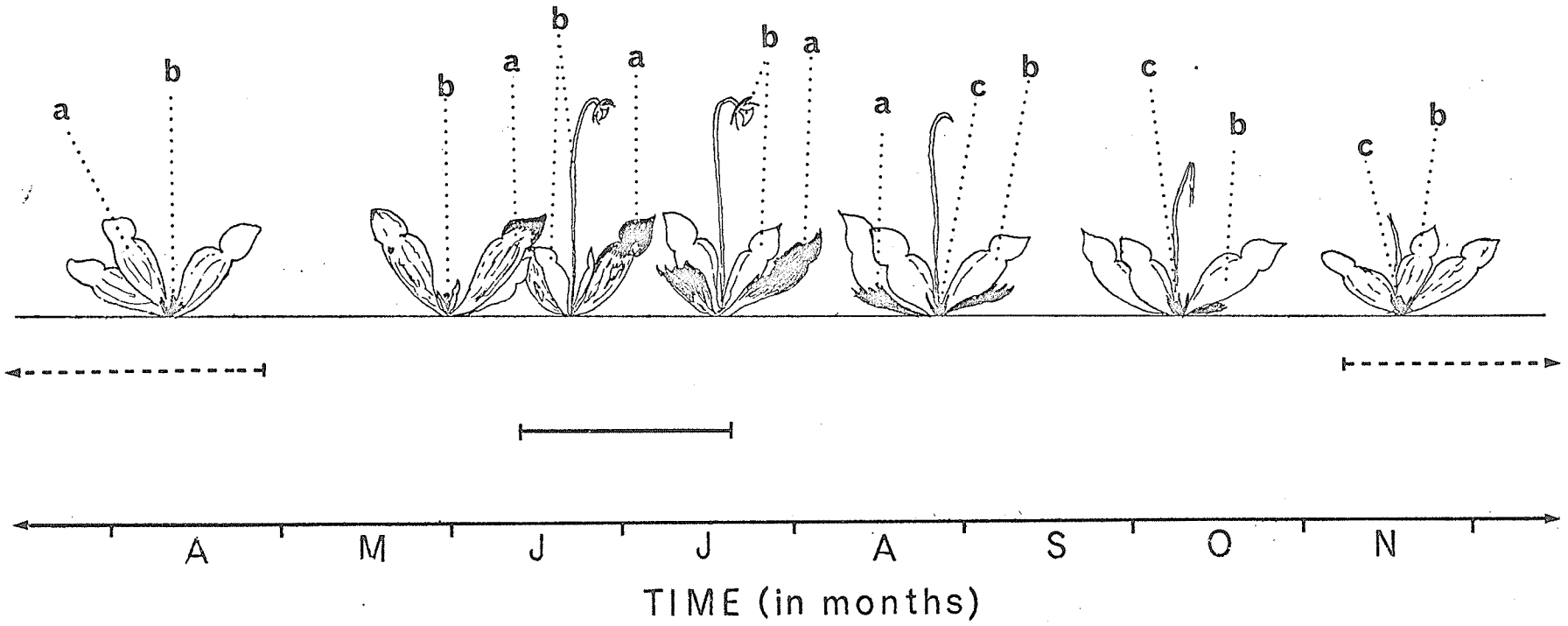
Figure 29. Young leaves as they appear in the fall. Environmental conditions will inhibit the growth at this stage until the following spring.

Figure 29

Figure 30. The flower bud, like the leaves, begins its development in late summer prior to its emergence the following spring. The developing flower bud can be found by removing the enshrouding leaves.

Figure 30

Figure 31. Succession of events in the growth cycle of *Sarracenia purpurea*. Overwintered leaves (a) which emerged the previous year begin to show signs of decay during June and by the end of July have degenerated to the point where they will no longer hold fluid. New leaves and flower buds (b) emerge about the end of May and reach maturity by the end of June/mid-July. These leaves will persist to the following spring. Next year's leaves (c) begin their growth about the middle of August but become dormant as fall approaches. These will emerge and mature the following spring. From about mid-June to mid-July, leaves of the previous year (a) and of the current year (b) are present. This is the period of inquiline transfer. Snow cover is present from early November through to the end of April.



a-Previous year's growth
b-Current year's growth
c-Next year's growth
----Snow cover
⊢——⊣ Period of inquiline transfer

Figure 31

Figure 32. Succession of events in the formation of a bog (after Smith, 1966).

A. Shallow lakes or ponds are gradually invaded by submerged, then floating plants. Accumulation of decomposed material raises the lake bottom. Soluble material precipitated by bacterial, chemical, or photosynthetic action forms a soft "false bottom".

B. Reeds, sedges, cotton grass, buckbean and marsh cinquefoil grow in the shallows. Sphagnum fills the open spaces between the plants. Decomposition forms a sedge peat mat which often extends outward over the water.

C. As the mat thickens cranberry, sweetgale, and bog rosemary appear. Accumulation of decaying sphagnum forms the basic material of the peat below. Increasing dryness allows the leather leaf to invade.

D. As the mat thickens and rises, plants intolerant of very wet conditions, leather leaf and laborador tea, become dominant. It is in this stage that *Sarracenia purpurea* is found.

E. First tree growth to follow is tamarck, then black spruce. The sphagnum mass eventually gives way to a woody peat.

F. The final stage is the formation of black humus and invasion of deciduous forest, or in the more northern region, conifers.

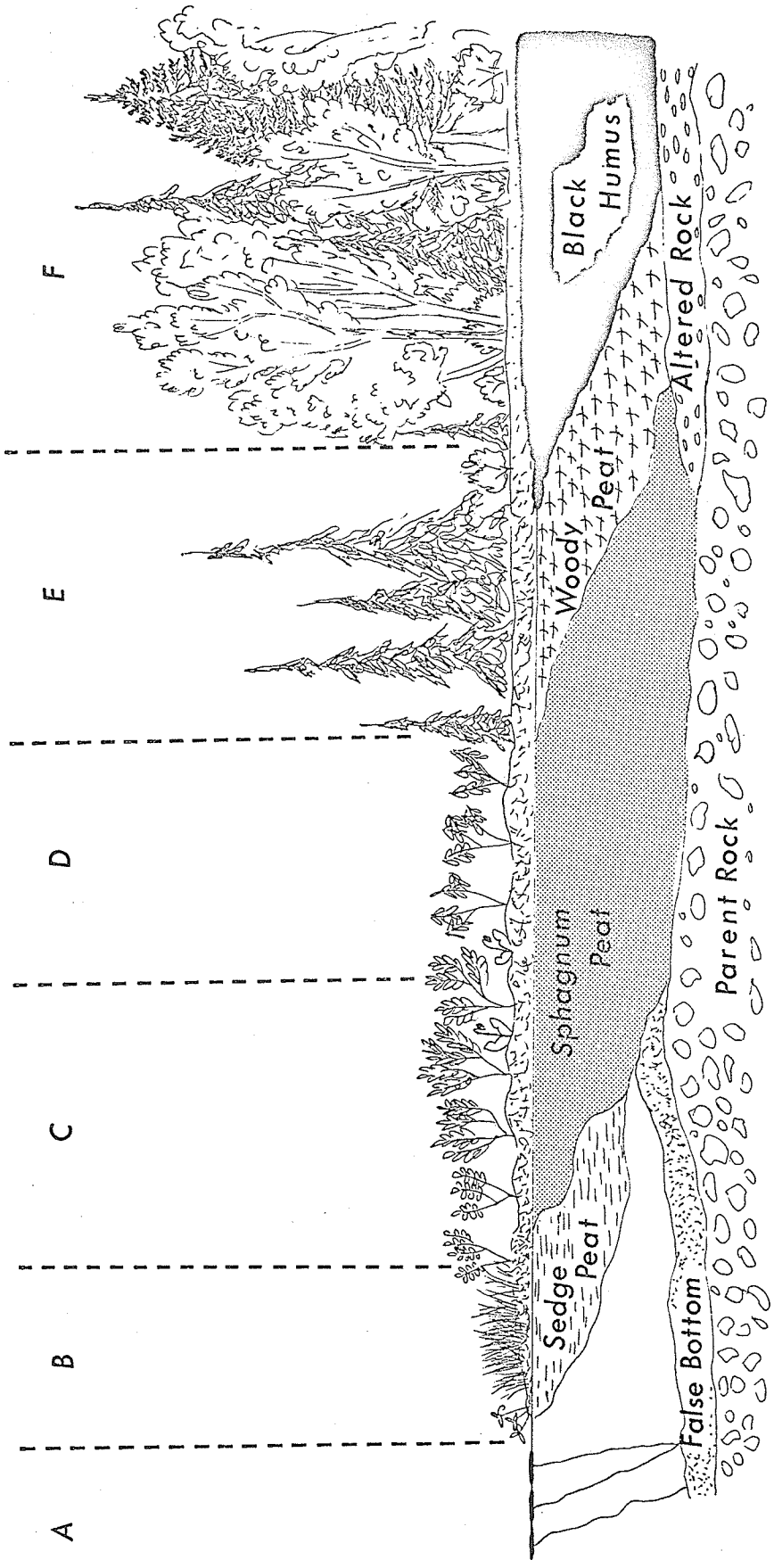

A
B
C
D
E
F
Black Humus
Altered Rock
Woody Peat
Sphagnum Peat
Sedge Peat
Parent Rock
False Bottom

Figure 32

Figure 33. The Kenora Bog--a lake edge bog exhibiting the typical succession zones shown in Figure 32 previous.

Figure 33

Figure 34. The Pinawa Bog--representative of succession Stage E with both tamarack and black spruce are the predominant trees.

Figure 35. The Pas Bog--an example of late stage E with black spruce the predominant tree growth.

Figure 34

Figure 35

Figure 36. *Sarracenia purpurea* growing on sphagnum hummocks in The Pas Bog.

Figure 36

Figure 37 Aerial view of the FIG ecological exclusion area, 1000 meters in diameter, located at the edge of the Pinawa Bog. Transition (b) from the drier deciduous forest (a) on the west side to the black spruce--tamarack(c) of the bog in the east is clearly visible by the changes in vegetation structure. Dotted lines denote the 100 meter square area in which part of this study was carried out. *Sarracenia purpurea* leaf samples were taken from grid areas one and two, while determination of plant species was conducted in grid area three. Location of temperature recorders are noted with "t".

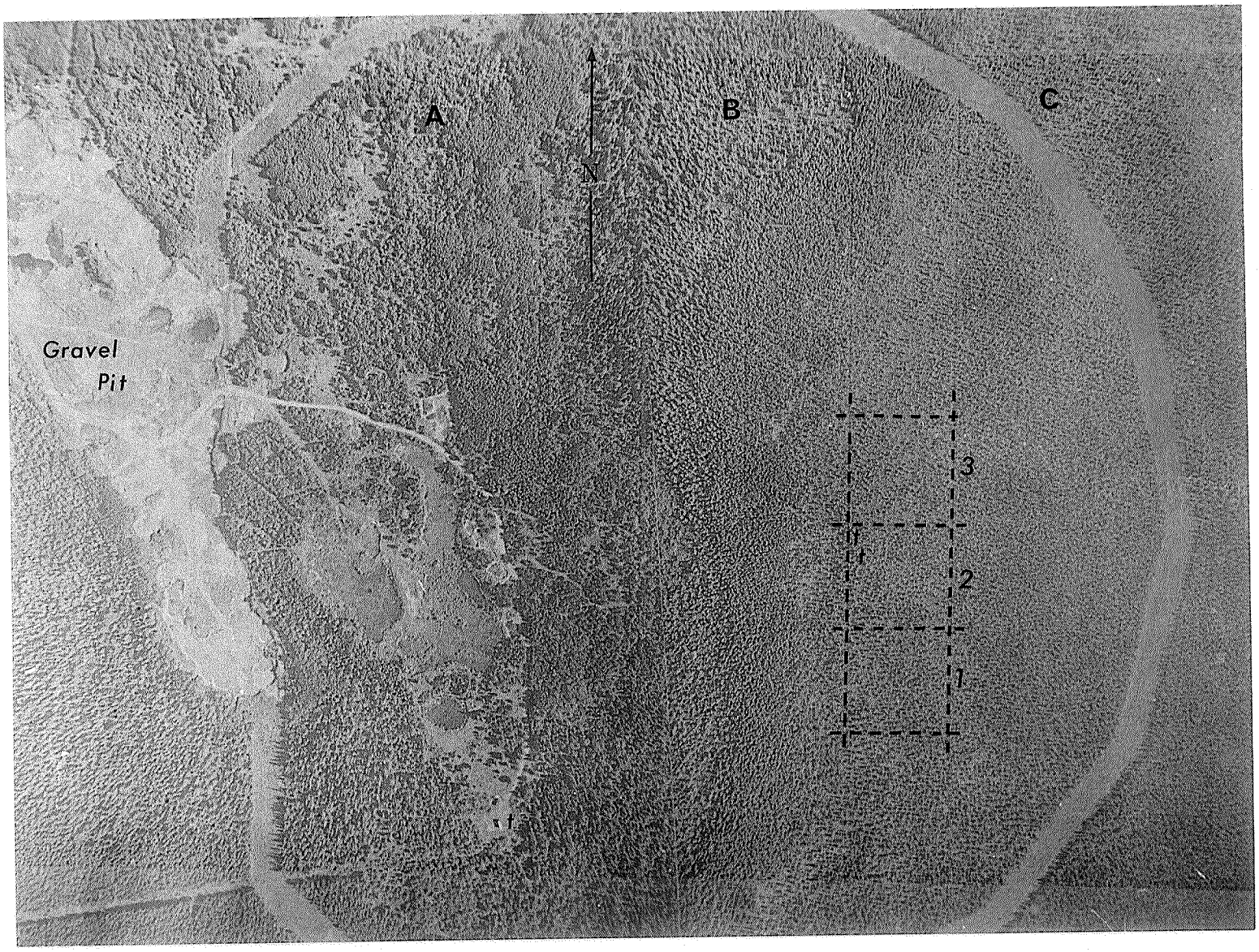

A
B
C
N
Gravel
Pit
3
2
1

Figure 38. Degree of aggregation of the various plant species in the Pinawa Bog based on D/d values: 0-1 Regular, 1-2 Random, greater than 2-- Aggregated.

A. *Vaccinium oxycoccus*

B. *Chamaedaphne calyculata*

C. *Ledum groenlandicum*

D. *Maianthenum canadense*

E. *Eriphorum angustifolium*

F. *Andromeda polifolia*

G. *Carex spp.*

H. *Betula glandulosa*

I. *Kalmia polifolia*

J. *Sarracenia purpurea*

K. *Picea mariana*

L. *Larix laricina*

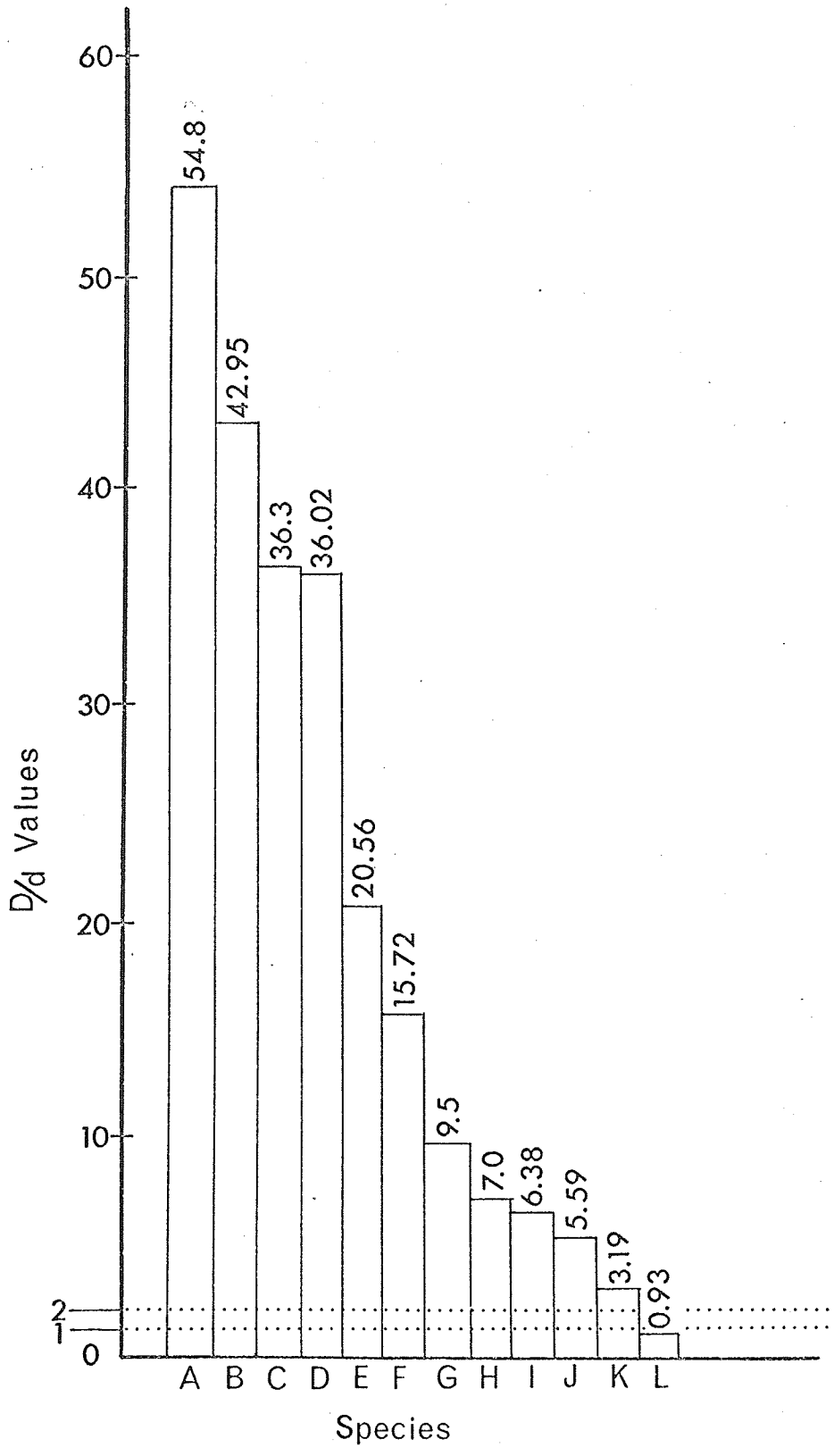

60
50
40
30
20
10
2
1
0
D/d Values
54.8
42.95
36.3
36.02
20.56
15.72
9.5
7.0
6.38
5.59
3.19
0.93
A B C D E F G H I J K L
Species

Figure 38

Figure 39. Diagramatic representation of FIG showing areas of High (H) and Low (L) tree densities. Low tree density and high numbers of *Sarracenia purpurea* are associated with the higher moisture found in the drainage ways of the bog.

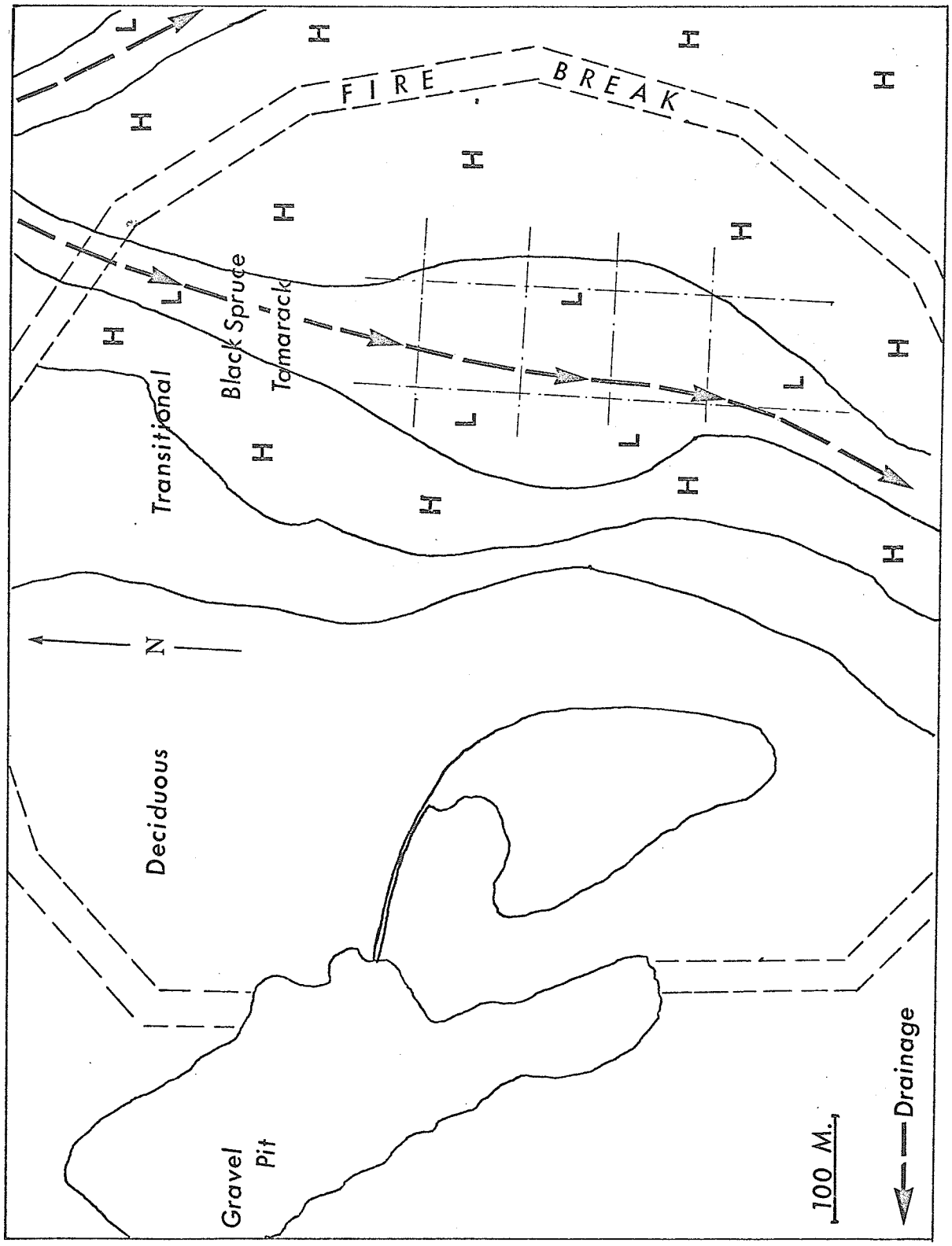

FIRE BREAK
Black Spruce
Tamarack
Transitional
Deciduous
Gravel Pit
N
100 M.
Drainage

Figure 39

Figure 40. Distribution of *Sarracenia purpurea* in Canada. Sources of the records from the western and northern extremities of the range (numbers 1 - 29) are given in Appendix D.

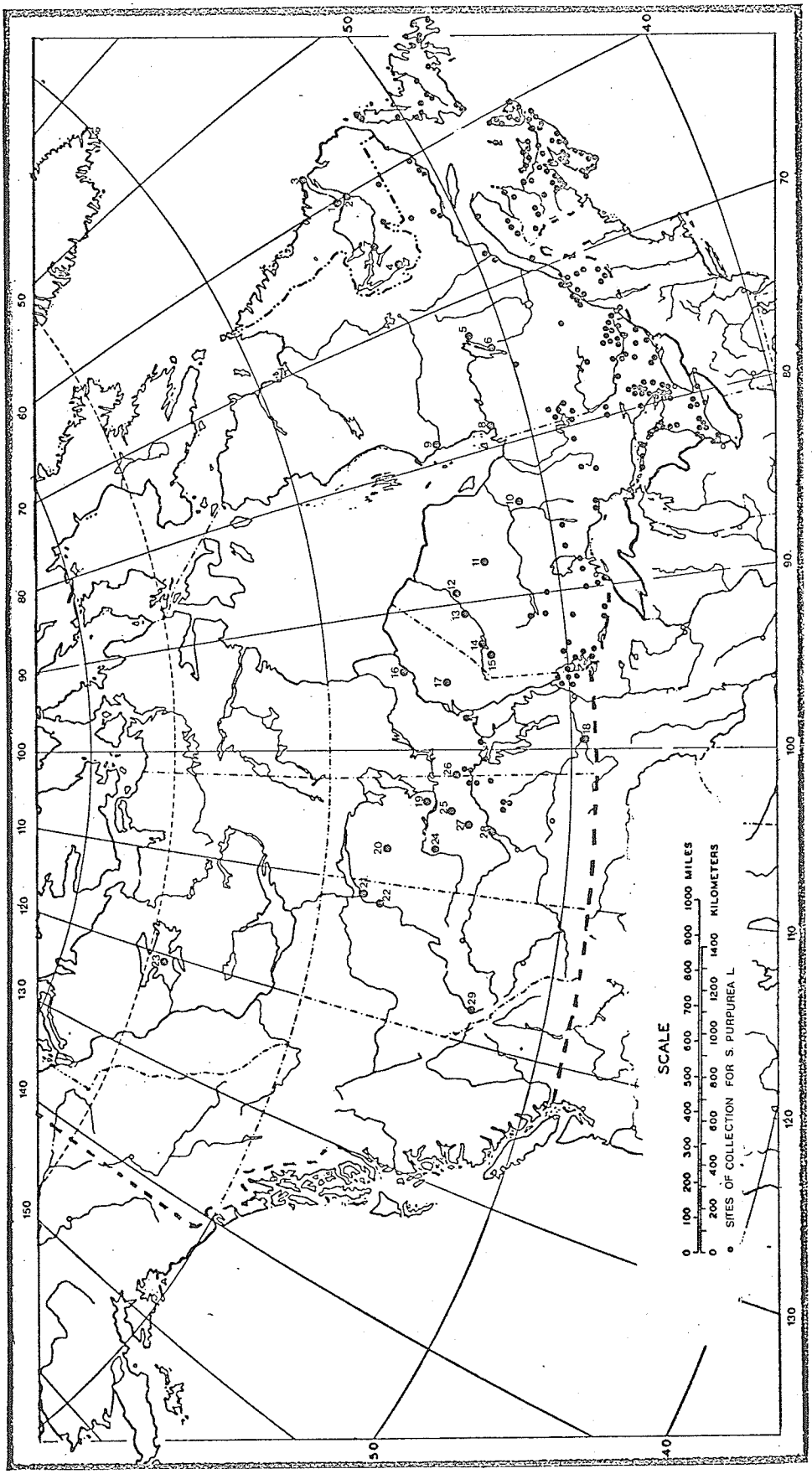

SCALE
0 100 200 300 400 500 600 700 800 900 1000 MILES
0 200 400 600 800 1000 1200 1400 KILOMETERS
SITES OF COLLECTION FOR S. PURPUREA L.

Figure 40

Figure 41. Distribution of *Sarracenia purpurea* in North America.

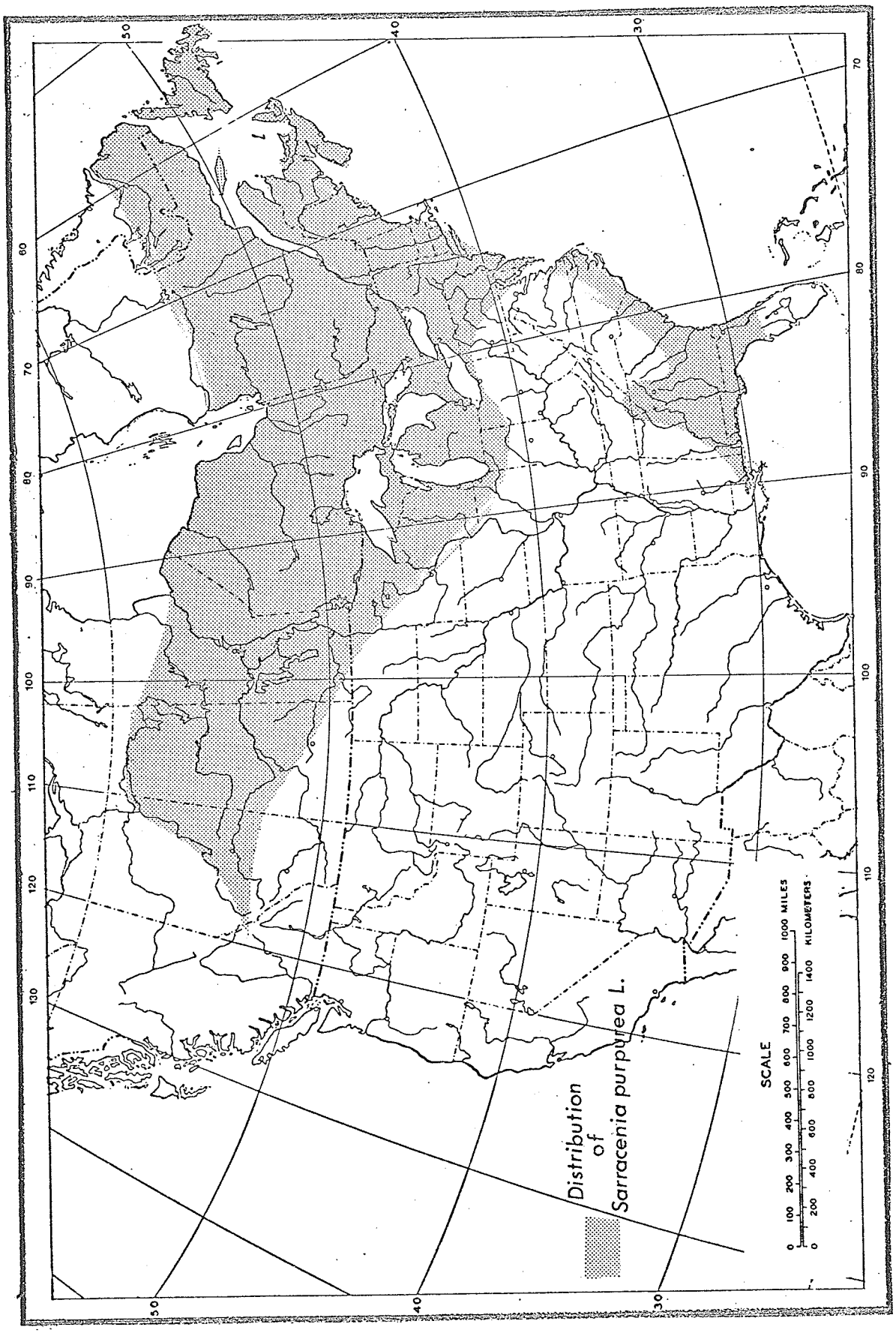

Distribution
of
Sarracenia purpurea L.
SCALE
0 100 200 300 400 500 600 700 800 900 1000 MILES
0 200 400 600 800 1000 1200 1400 KILOMETERS

Figure 41

Figure 42. Flower of *Sarracenia purpurea* infected by the larvae of *Endothenia daeckeana* Krt.

Figure 43. Normal uninfected flower of *Sarracenia purpurea* taken at same time of year.

Figure 42

Figure 43

Figure 44. Leaf of *Sarracenia purpurea* showing the groove in the region of the collar made by the larvae of the moth, *Exyra rolandiana* Grt.

Figure 45. A. Leaf with groove in the collar.

B. Leaf with collar sealed after the upper portion has died and withered.

C. Normal leaf.

Figure 44

Figure 45

Figure 46. Ingestion stage of *Wyeomyia smithii* third instar larvae fed on China Ink.

A. up to one-half full.

B. one-half to three-quarters full.

C. three-quarters full to glutted.

Figure 47. Replacement stage of *Wyeomyia smithii* third instar larvae glutted on China Ink then fed nutritive diet.

D. up to one-half replacement.

E. one-half to three-quarters replacement.

F. three-quarters to full replacement.

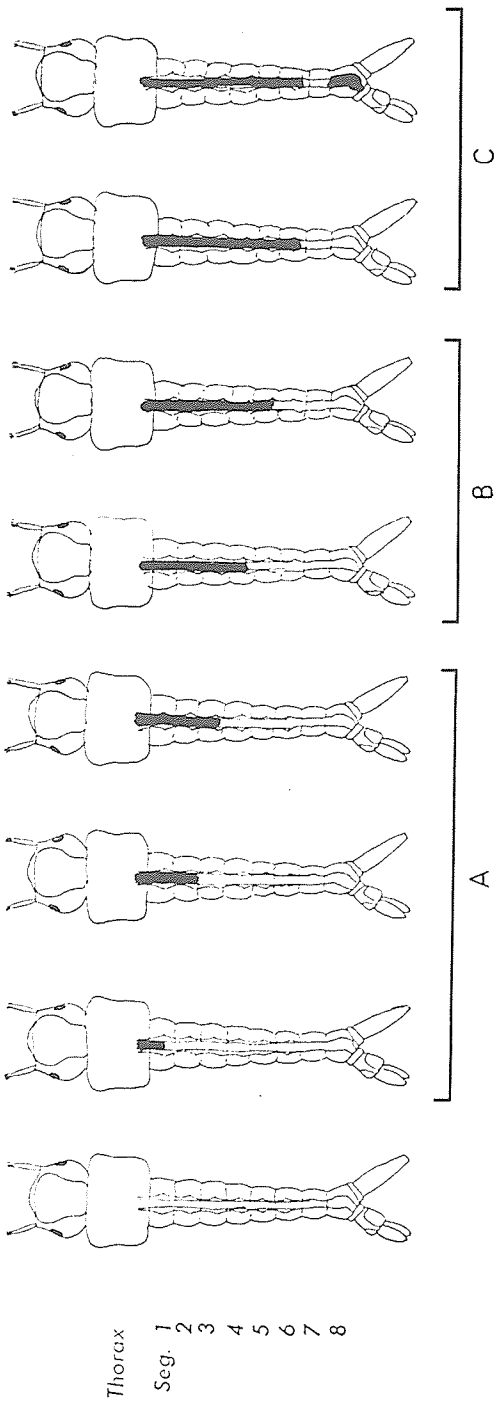


Figure 46

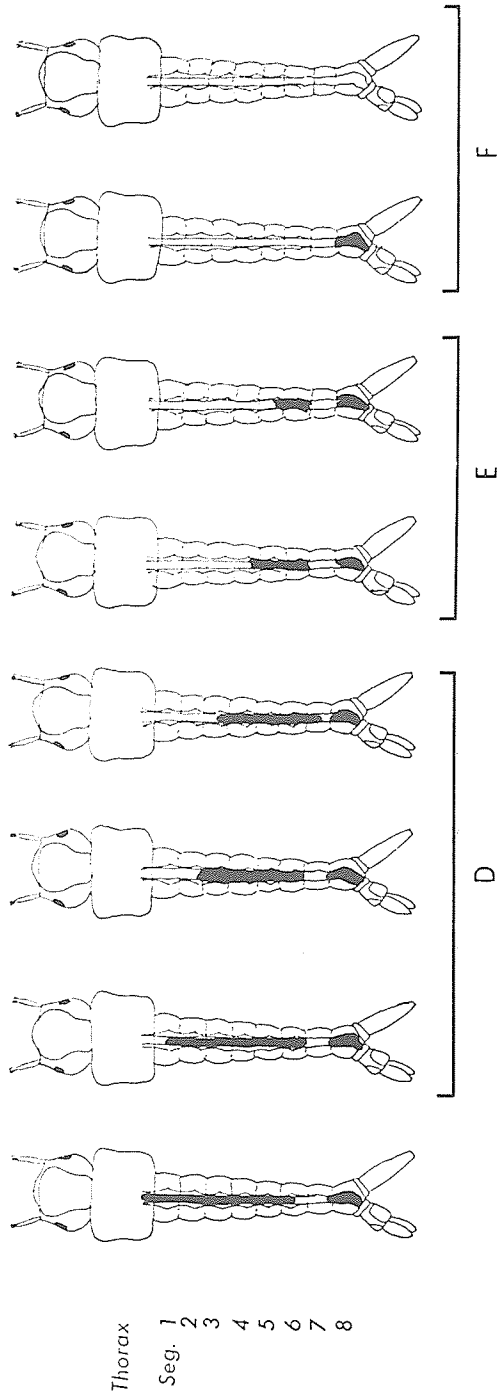


Figure 47

Figure 48. Ingestion rates of three groups of larvae fed China Ink expressed as frequency percent against time in days.

A. up to one-half full.

B. one-half to three-quarters full.

C. three-quarters full to glutted.

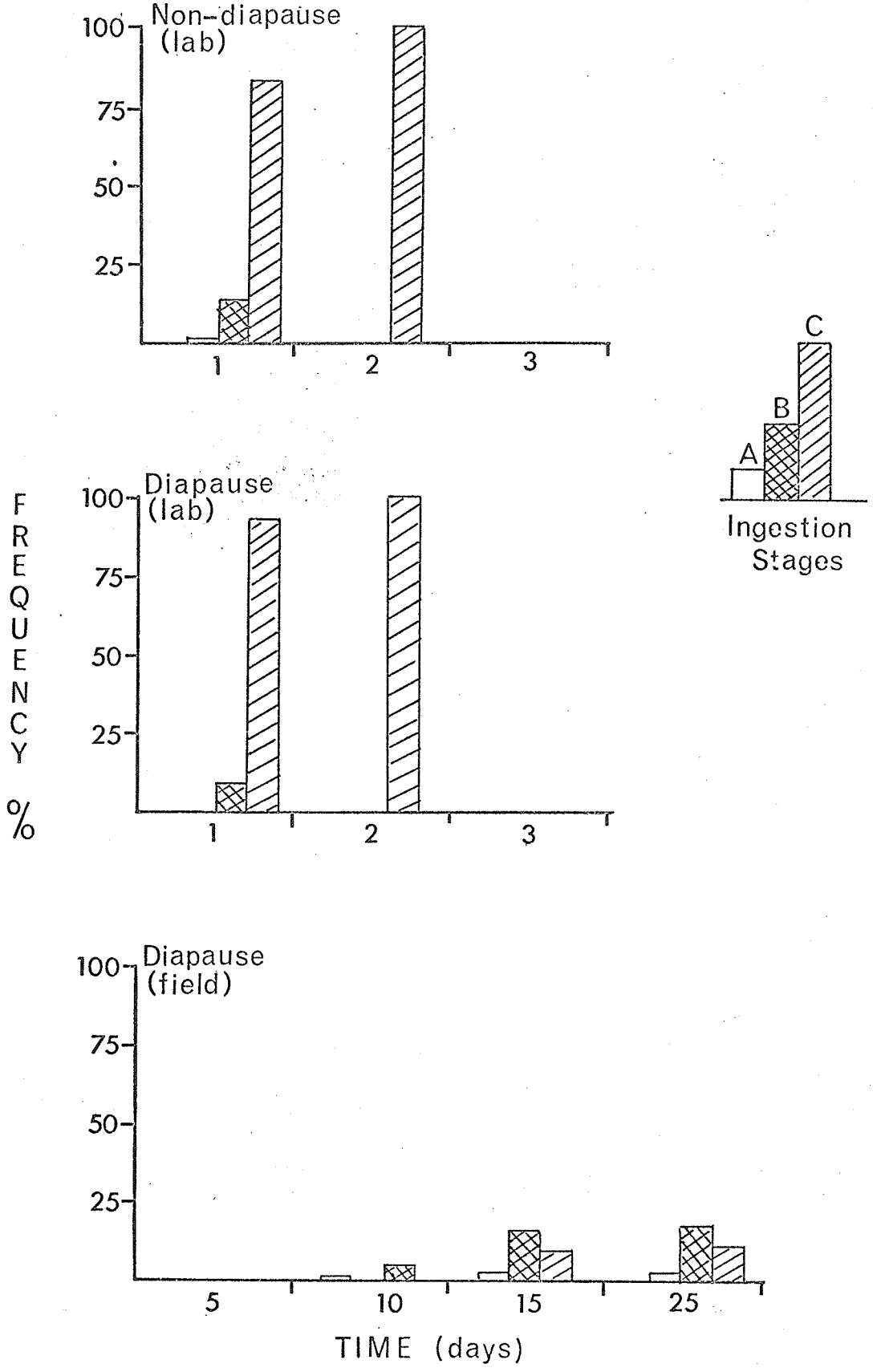

Non-diapause
(lab)
100
75
50
25
1
2
3
Diapause
(lab)
FREQUENCY %
Diapause
(field)
5
10
15
25
TIME (days)
A
B
C
Ingestion
Stages

Figure 48

Figure 49. Replacement rates in three larval groups first glutted on China Ink then fed nutritive diet. Expressed as frequency percent against time in hours.

D. up to one-half replacement.

E. one half to three-quarters replacement.

F. three-quarters to full replacement.

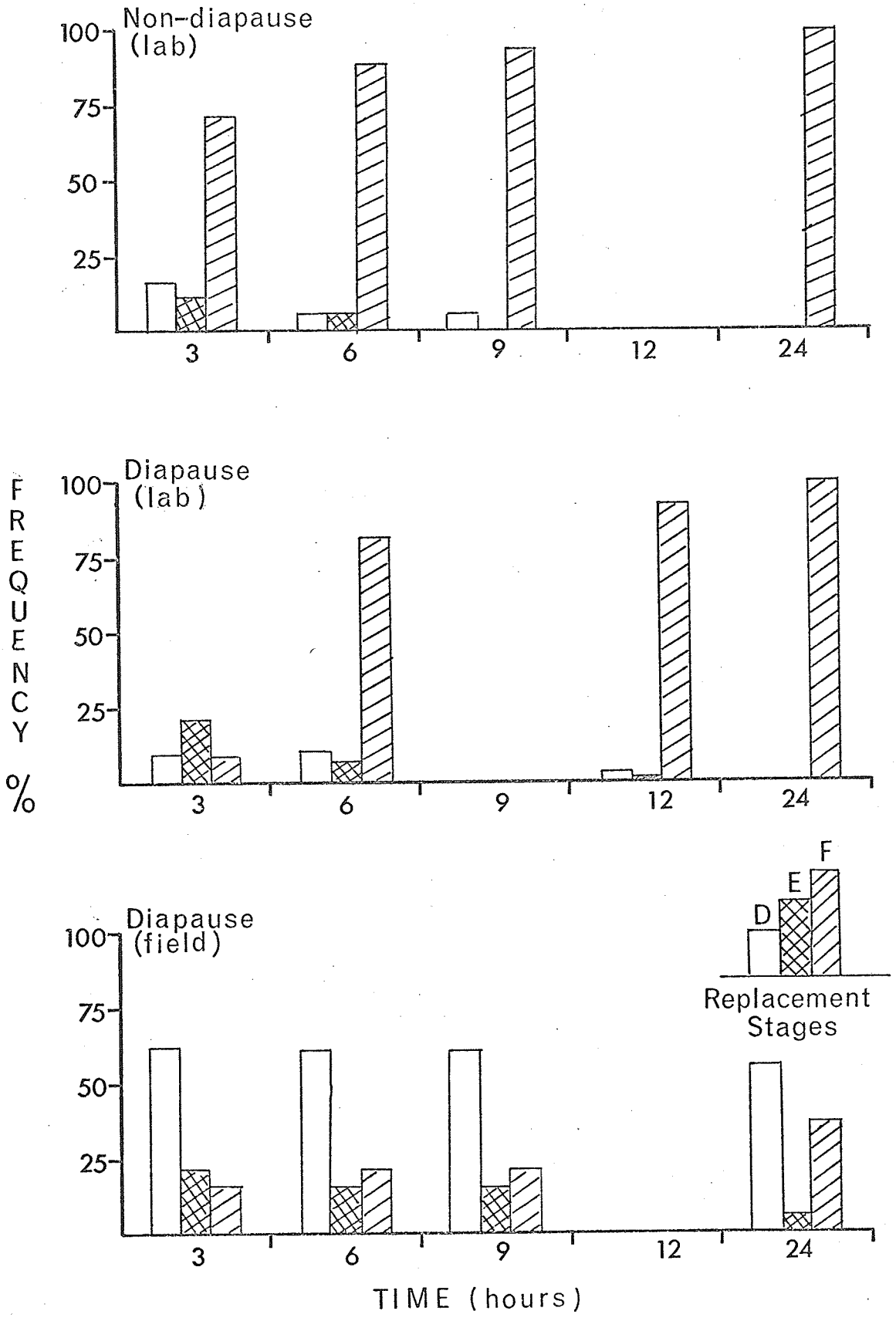

Non-diapause
(lab)
100
75
50
25
3
6
9
12
24
Diapause
(lab)
FREQUENCY %
Diapause
(field)
D
E
F
Replacement
Stages
TIME (hours)

Figure 49

Figure 50. Uptake of ^{137}Cs by *Wyeomyia smithii* third instar larvae fed $^{137}Cesium$ labeled dog food. Mean ± one standard deviation are plotted.

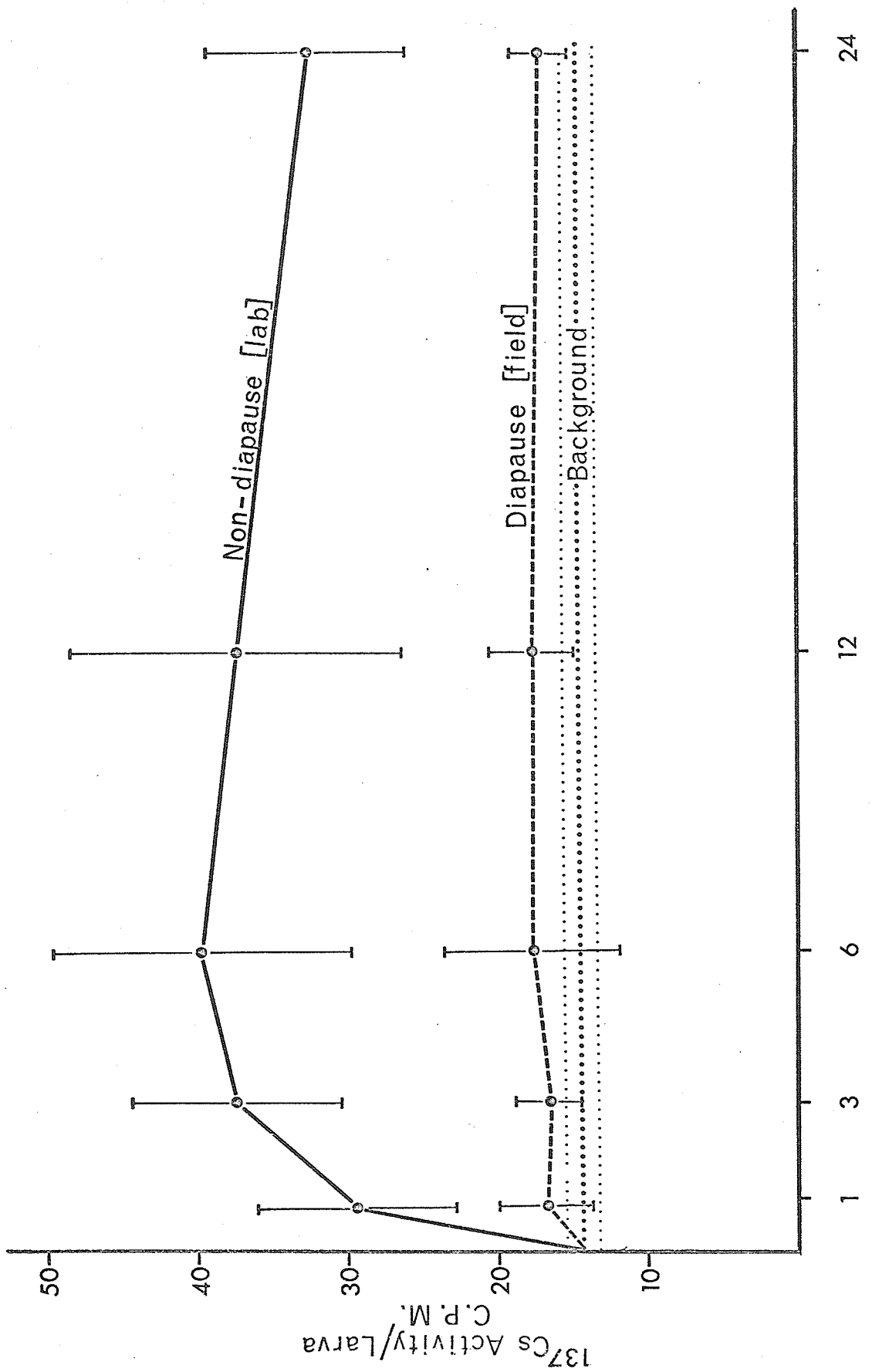

Non-diapause [lab]
Diapause [field]
Background
50
40
30
20
10
1
3
6
12
24
TIME [hours]
137Cs Activity/Larva
C.P.M.

Figure 50

Figure 51. Uptake of ^{137}Cs by *Wyeomyia smithii* third instar larvae reared in nutrient-free medium. Mean ± standard deviation are plotted.

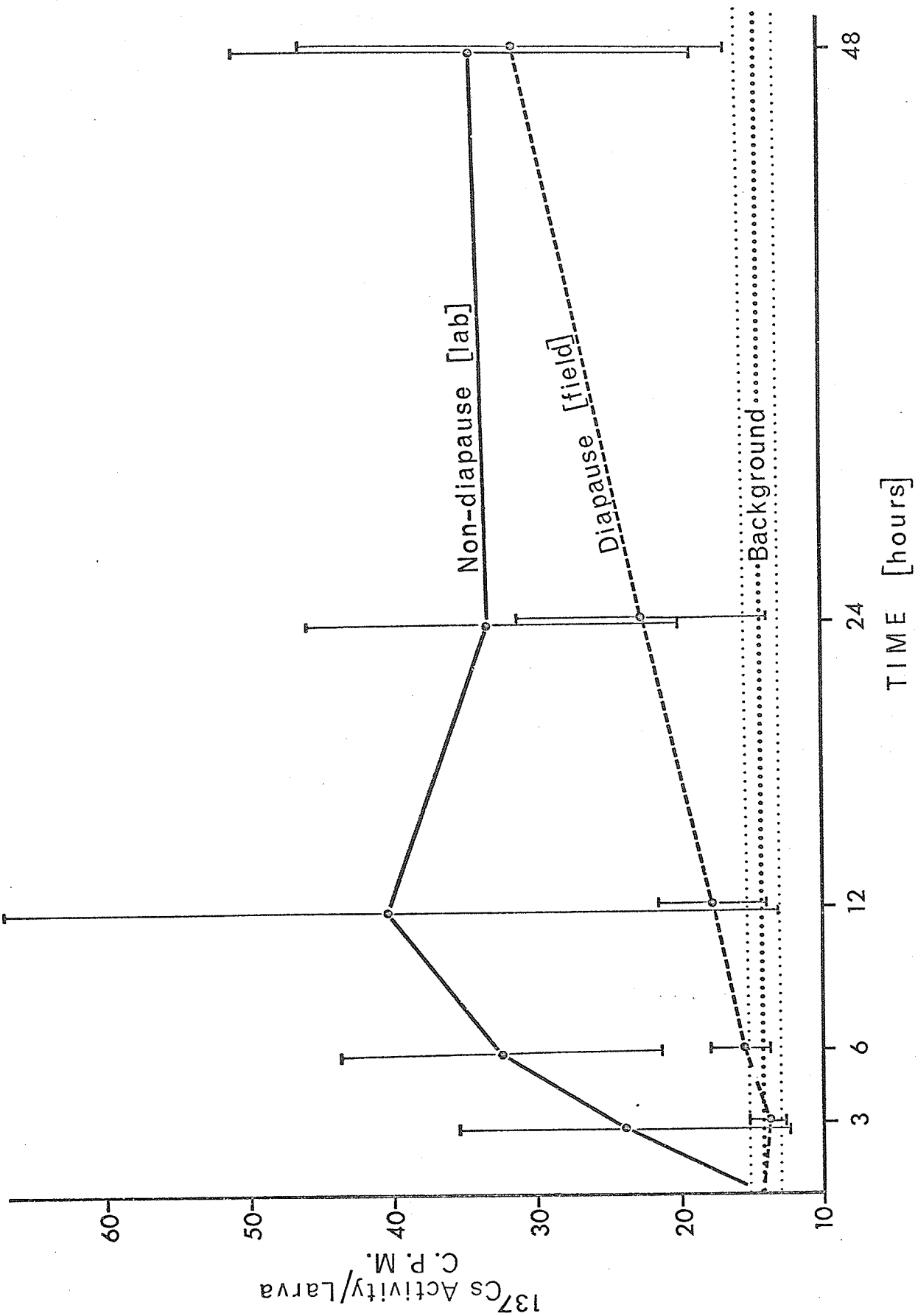

137Cs Activity/Larva
C. P. M.
60
50
40
30
20
10
3
6
12
24
48
TIME [hours]
Non-diapause [lab]
Diapause [field]
Background

Figure 51

Figure 52. Percent of larvae molting to fourth instar after forty days (25°C) at various daily photoperiods.

A. Egg pretreated at 18L:6D at 27°C, first, second, and third instars reared at various photoperiods.

B. Egg and first instar pretreated at 18L:6D at 27°C, second and third instars reared at various photoperiods.

C. Egg, first and second instars pretreated at 18L:6D at 27°C, third instar reared at various photoperiods.

Induction of diapause is noted as a failure to molt to fourth instar after forty days.

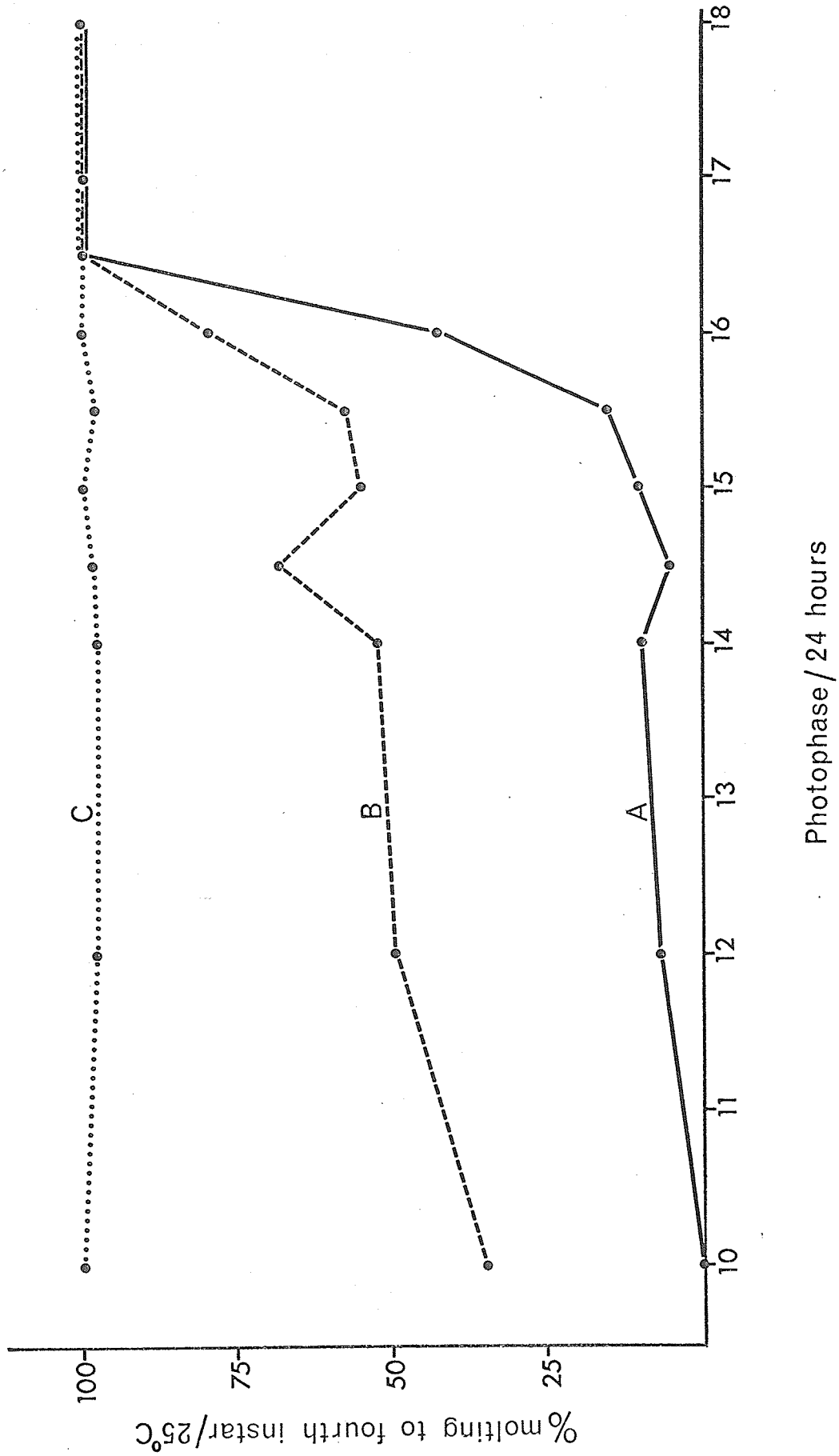

% molting to fourth instar/25°C
100
75
50
25
C
B
A
10
11
12
13
14
15
16
17
18
Photophase / 24 hours

Figure 52

Figure 53. Percent of third instar larvae molting to fourth instar (terminating diapause) after thirty days (20°C) at various daily photoperiods.

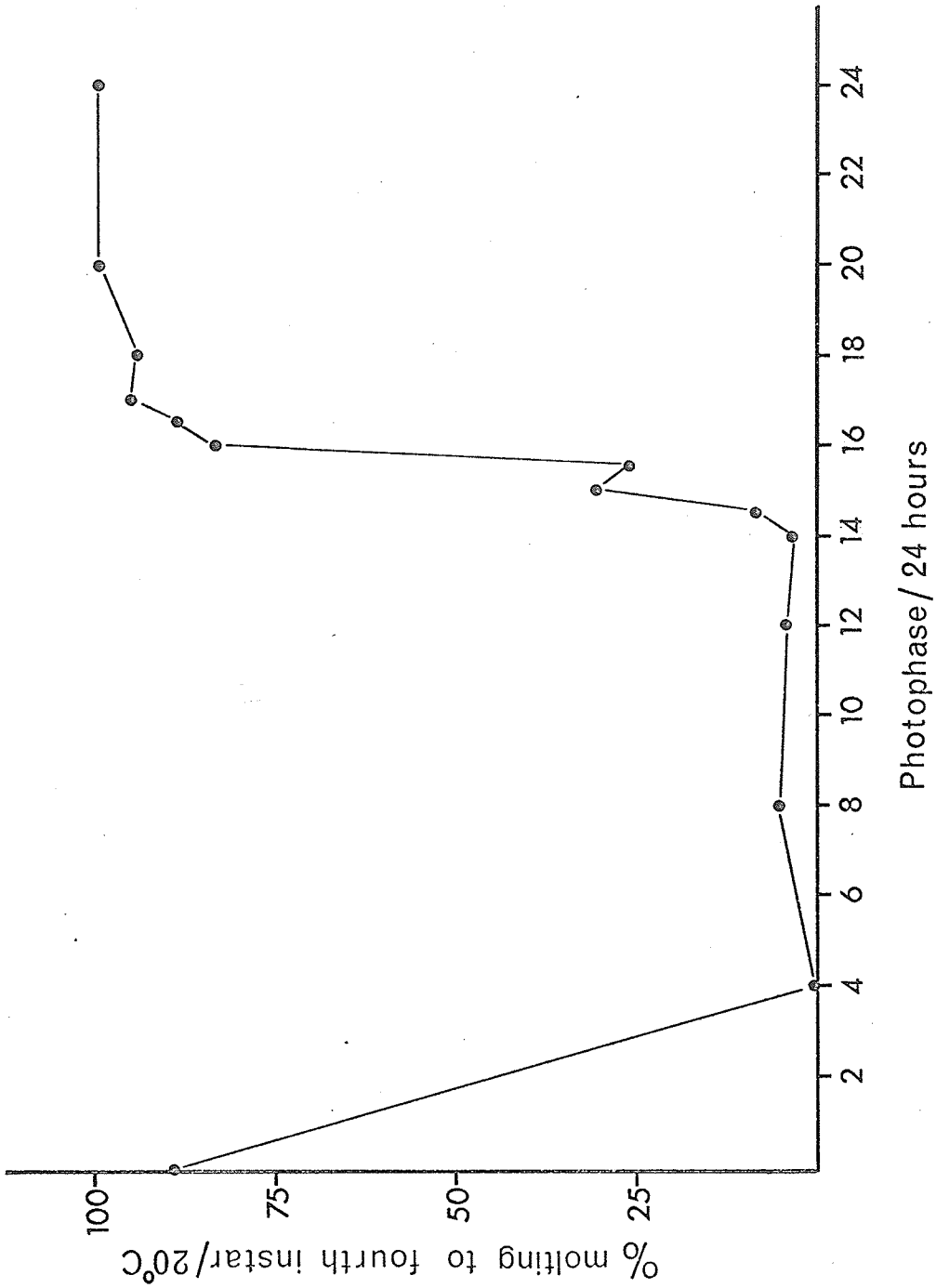

% molting to fourth instar/20°C
100
75
50
25
2
4
6
8
10
12
14
16
18
20
22
24
Photophase/24 hours

Figure 53

Figure 54. Percentage of three groups of third instar larvae molting to fourth instar at various temperatures when reared at a non-diapausing photoperiod (18L:6D).

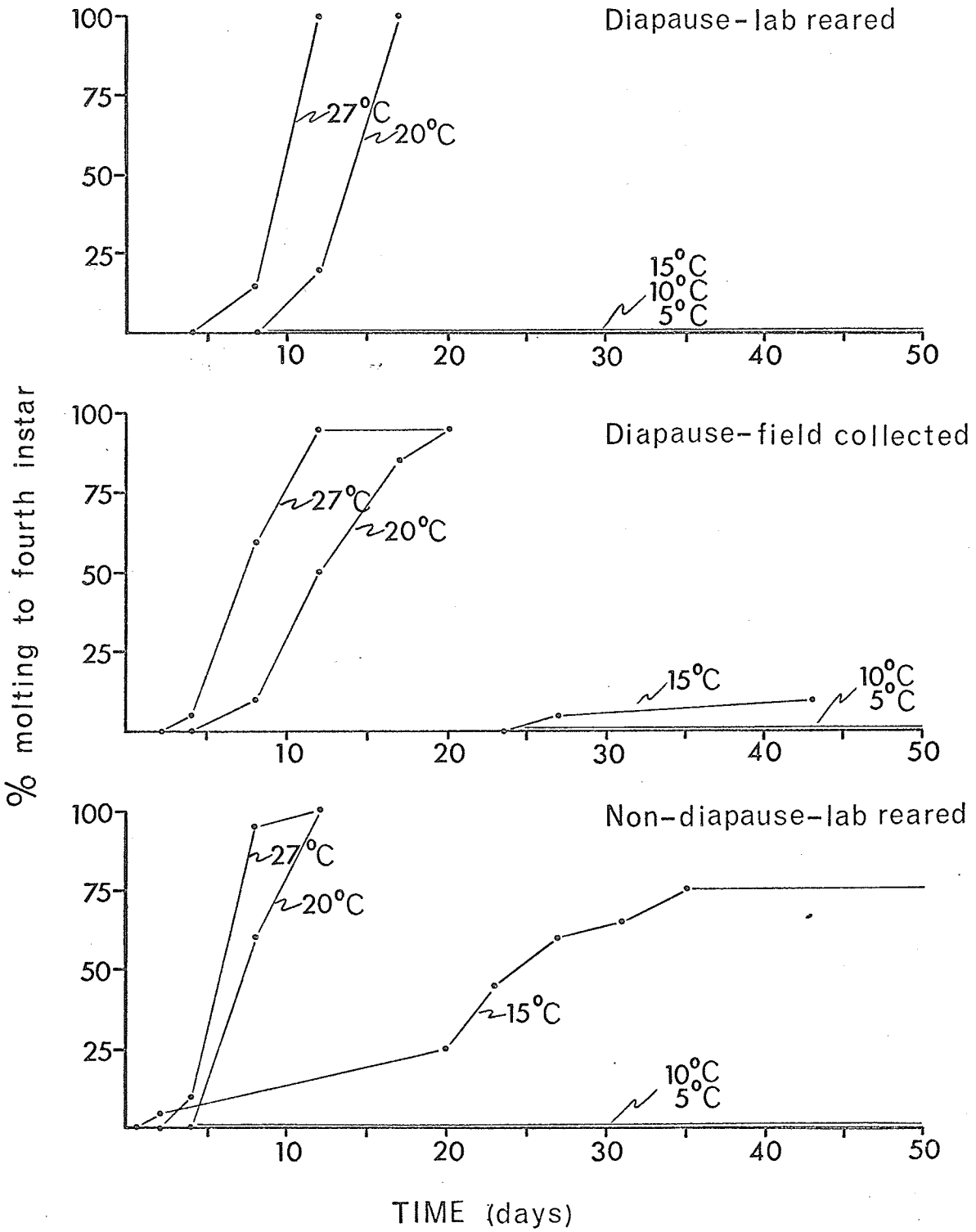

Diapause-lab reared
Diapause-field collected
Non-diapause-lab reared
27°C
20°C
15°C
10°C
5°C
100
75
50
25
10
20
30
40
50
% molting to fourth instar
TIME (days)

Figure 54

Figure 55. Day length curve (sunlight or daylight plus civil twilight) for Pinawa, Manitoba (50°15'N - 95°50'W). The critical photoperiods required for termination (T) and induction (I) of diapause for *Wyeomyia smithii* are indicated (14 1/2 hours light per day).

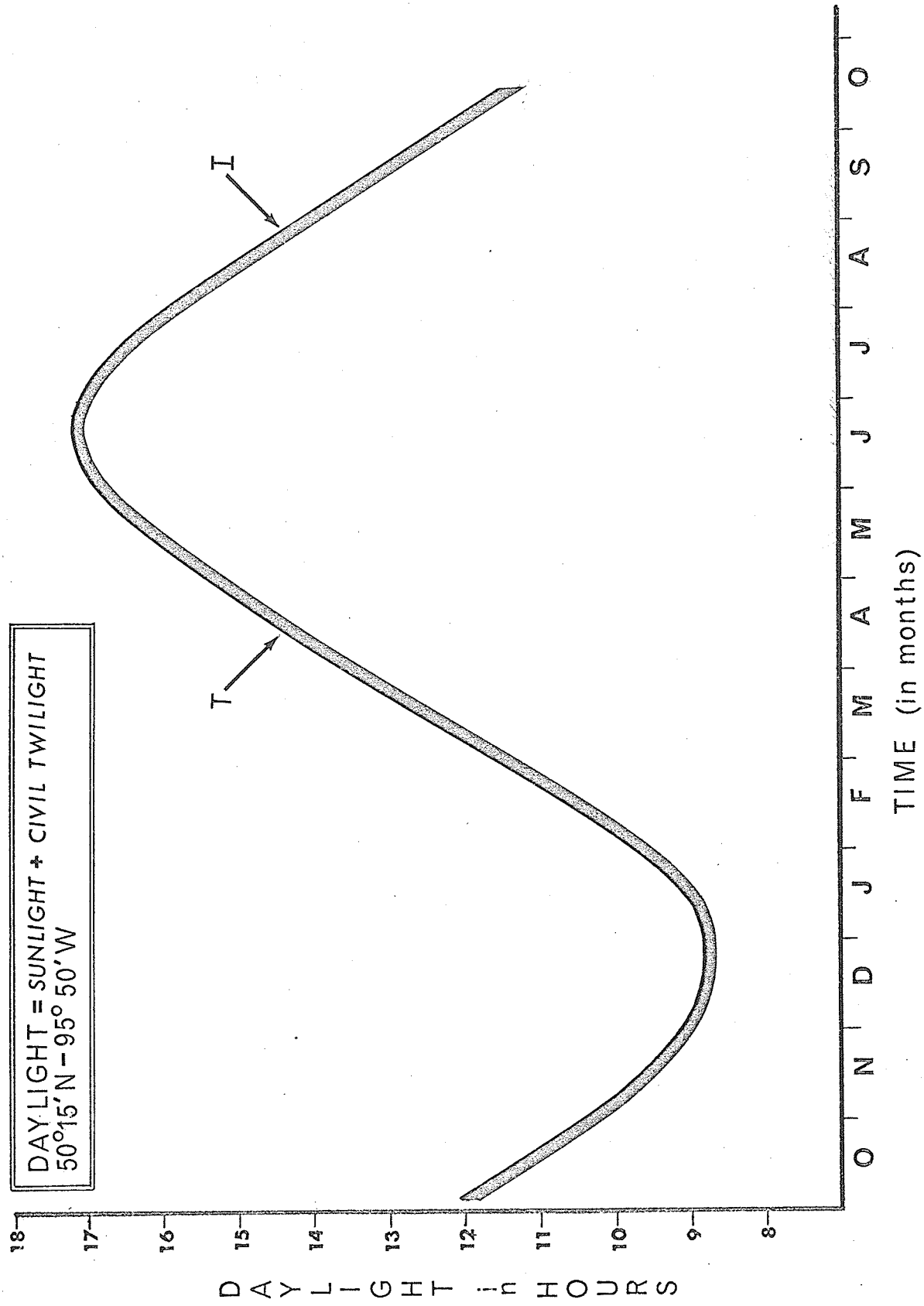

DAYLIGHT = SUNLIGHT + CIVIL TWILIGHT
50°15'N - 95° 50'W
I
T
DAYLIGHT in HOURS
18
17
16
15
14
13
12
11
10
9
8
O
N
D
J
F
M
A
M
J
J
A
S
O
TIME (in months)

Figure 55

Figure 56. Percent survival of non-conditioned diapausing third instar larvae at various low and sub-zero temperatures (-10°C trial not available due to equipment malfunction).

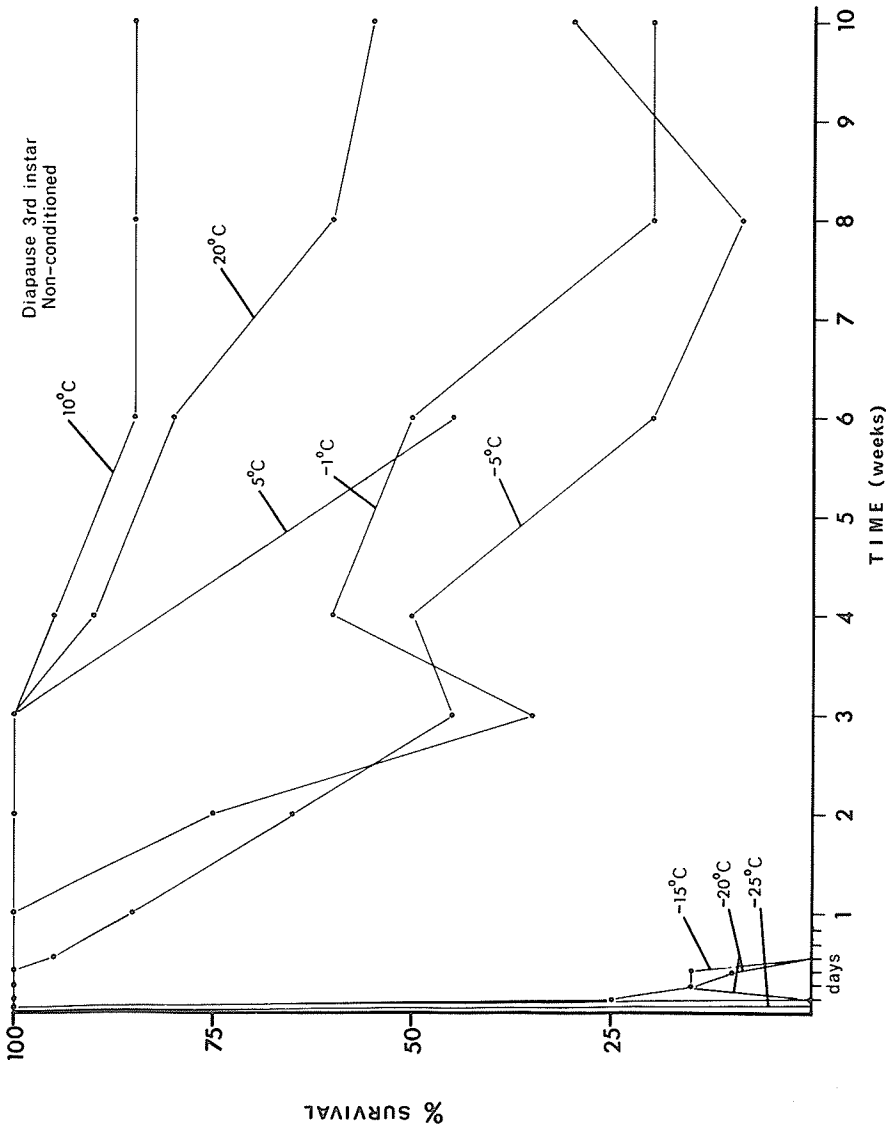

Diapause 3rd instar
Non-conditioned
10°C
20°C
5°C
-1°C
-5°C
-15°C
-20°C
-25°C
100
75
50
25
% SURVIVAL
days
1
2
3
4
5
6
7
8
9
10
TIME (weeks)

Figure 56

Figure 57. Percent survival of pre-conditioned diapausing third instar larvae at various low and sub-zero temperatures.

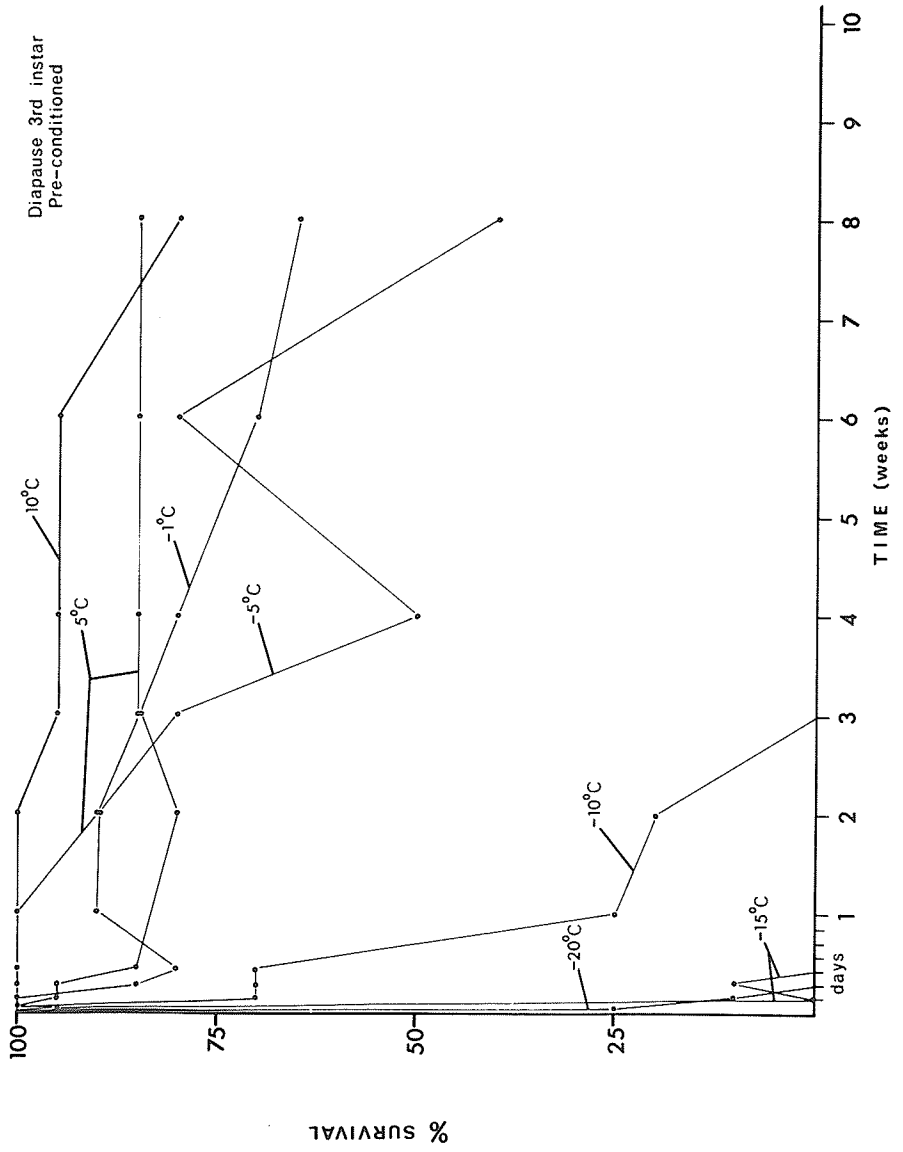

Diapause 3rd instar
Pre-conditioned
10°C
5°C
-1°C
-5°C
-10°C
-20°C
-15°C
days
1
2
3
4
5
6
7
8
9
10
TIME (weeks)
100
75
50
25
% SURVIVAL

Figure 57

Figure 58. Percent survival of non-conditioned, non-diapausing third instar larvae at various low and sub-zero temperatures.

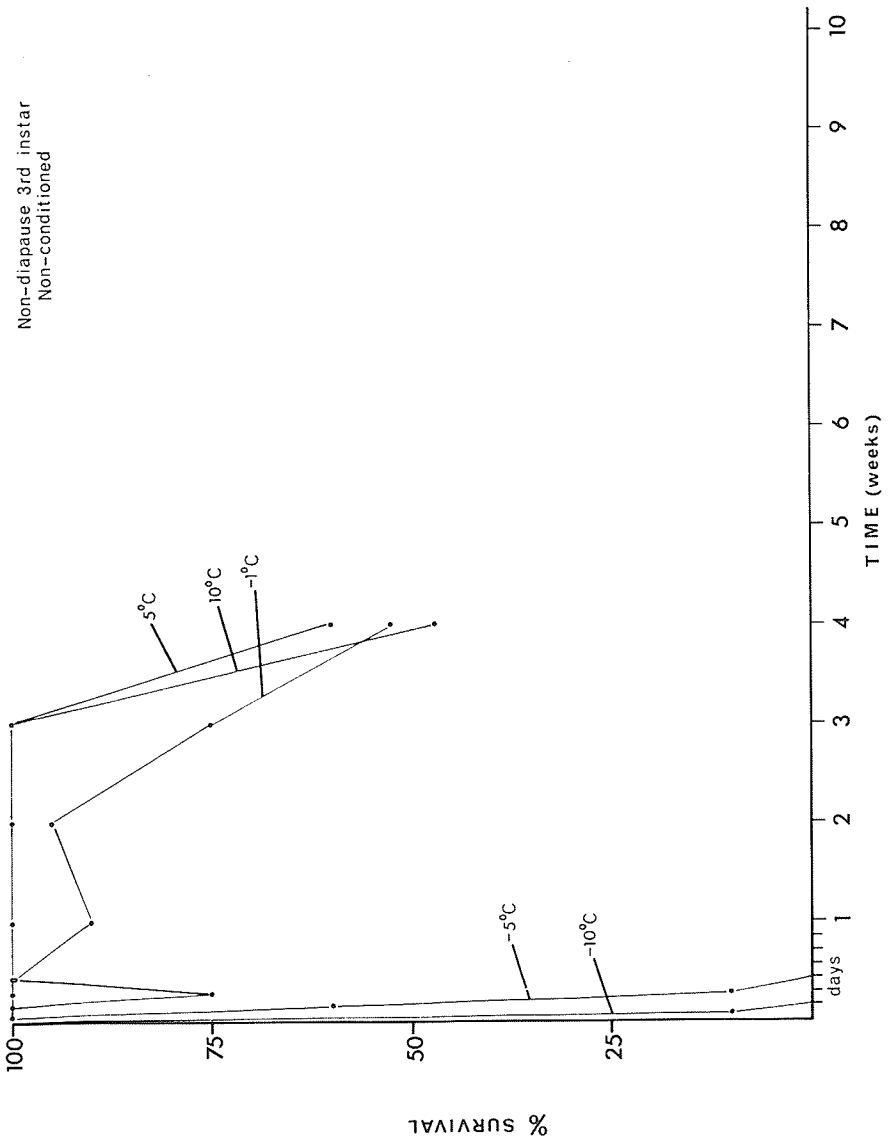

Non-diapause 3rd instar
Non-conditioned
5°C
10°C
-1°C
-5°C
-10°C
100
75
50
25
% SURVIVAL
days
1
2
3
4
5
6
7
8
9
10
TIME (weeks)

Figure 58

Figure 59. Comparison of supercooling temperatures in six different larval groups.

D3--Diapause third instar held at 12L:12D for three months.

ND3--Non-diapause third instar reared at 18L:6D at 27°C.

D3F--Diapause third instar, field-collected prior to trials (29/12/70).

D3H--Diapause third instar held at 12L:12D and and 20°C for one month; 10°C for two months and 5°C for one month.

II--second instar reared at 18L:6D at 27°C.

IV--fourth instar reared at 18L:6D at 27°C.

Supercooling temperature of the larvae were grouped (0° to -5°C, -5° to -10°C, -10° to -15°C, -15° to -20°C) and expressed as a percent. Mean ± one standard deviation for each group is also given.

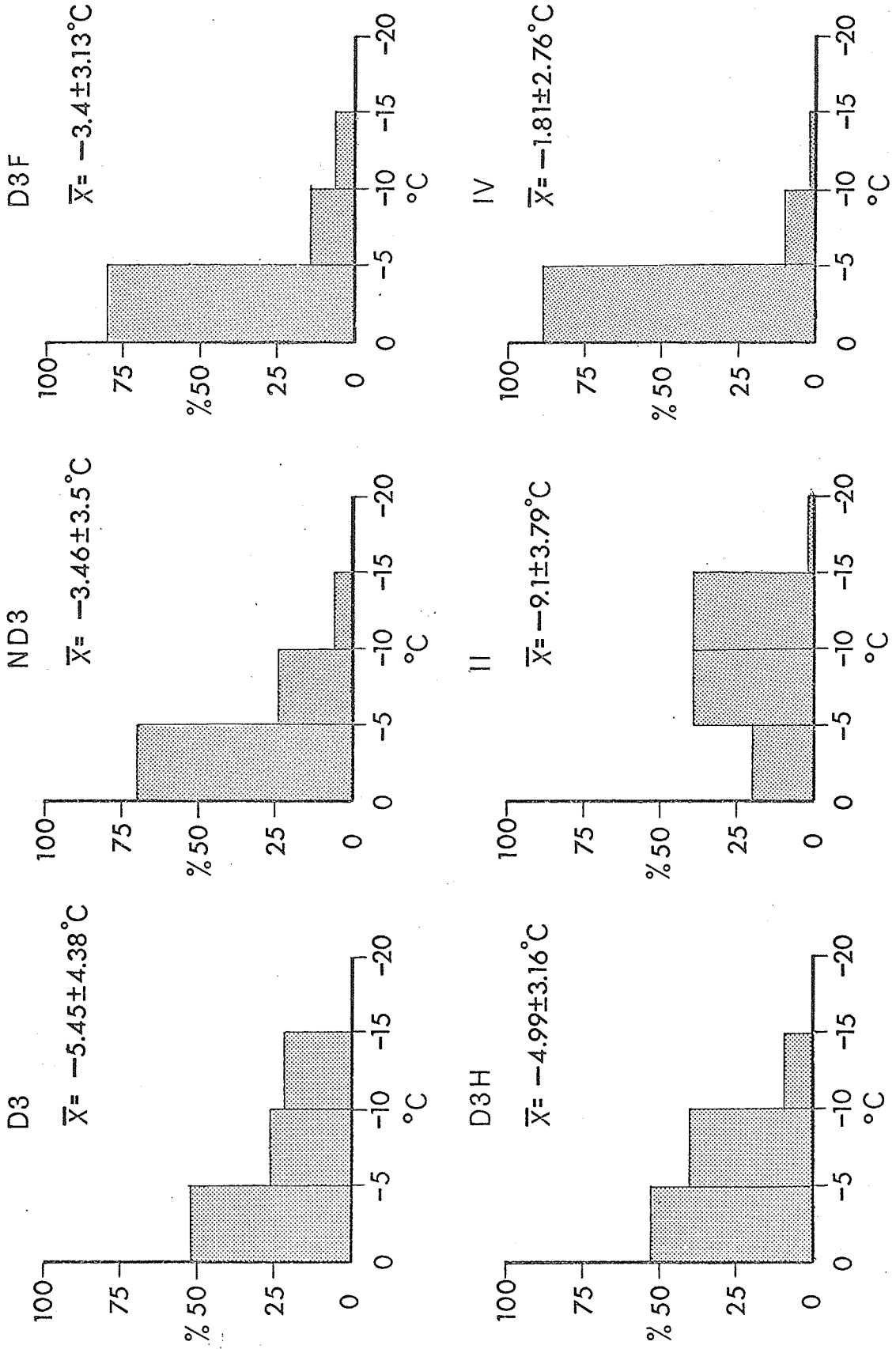

D3
$\bar{X}$= −5.45±4.38°C
ND3
$\bar{X}$= −3.46±3.5°C
D3F
$\bar{X}$= −3.4±3.13°C
II
$\bar{X}$= −9.1±3.79°C
D3H
$\bar{X}$= −4.99±3.16°C
IV
$\bar{X}$= −1.81±2.76°C
100
75
% 50
25
0
0
-5
-10
-15
-20
°C

Figure 59

Figure 60. Five day mean temperatures for air and sphagnum (at the level where the larvae occur) in the Pinawa Bog October 1, 1969 to October 18, 1970. The effect of the snow cover in preventing sphagnum (and larval) temperatures from reaching the extremes the air temperatures reach during the winter is clearly deomonstrated.

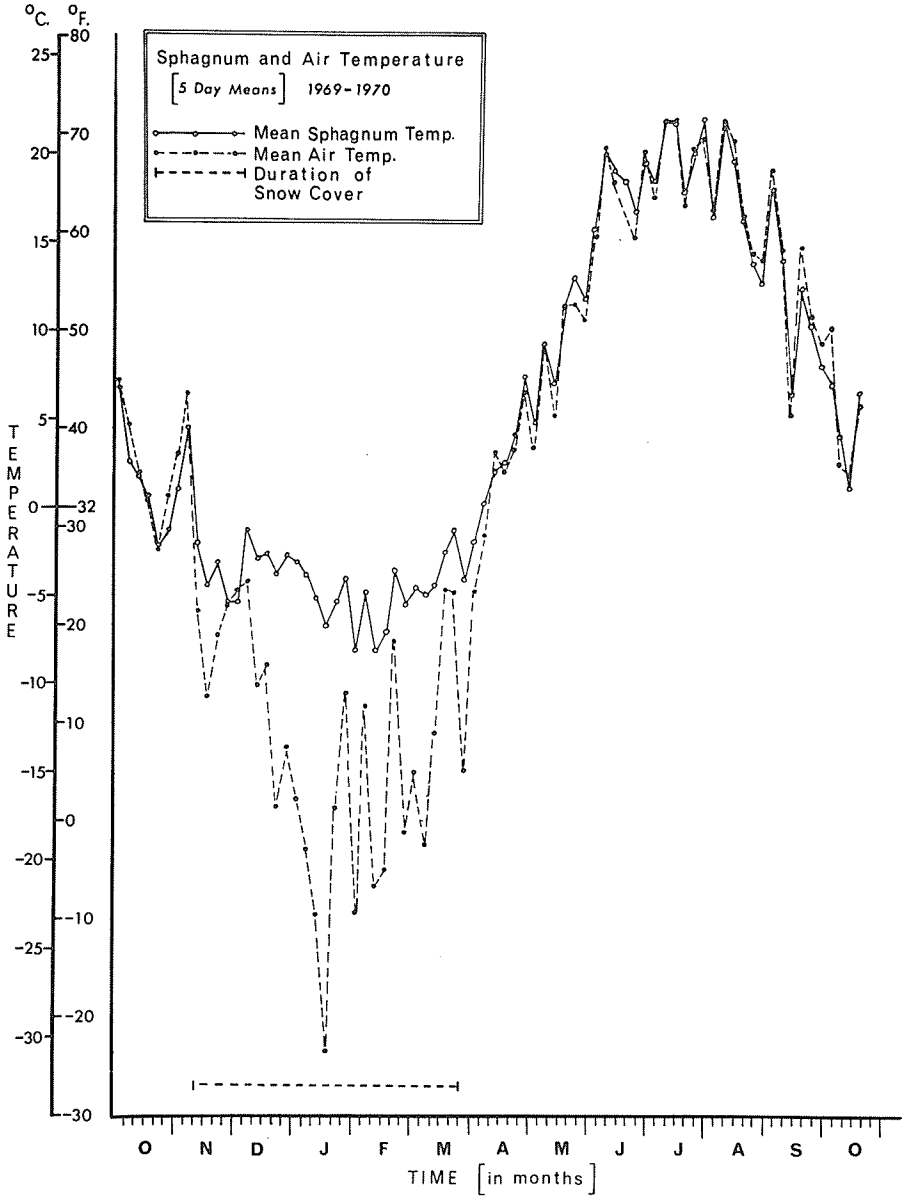

°C.
°F.
Sphagnum and Air Temperature
[5 Day Means] 1969-1970
Mean Sphagnum Temp.
Mean Air Temp.
Duration of Snow Cover
TEMPERATURE
25
20
15
10
5
0
-5
-10
-15
-20
-25
-30
80
70
60
50
40
32
30
20
10
0
-10
-20
O N D J F M A M J J A S O
TIME [in months]

Figure 60

Figure 61. Snow depth and duration of snow cover for Pinawa Bog during the winter 1969-1970.

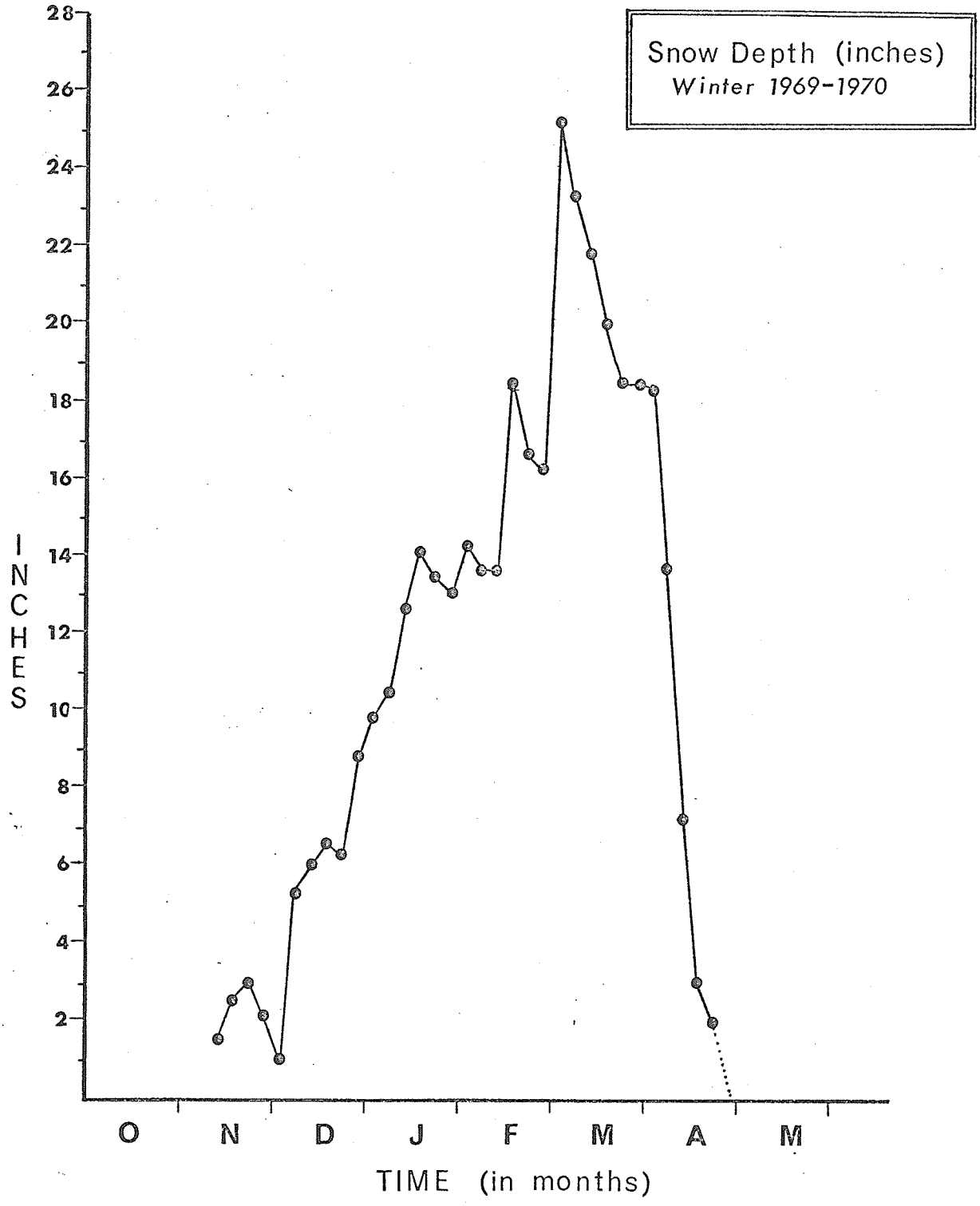

Snow Depth (inches)
Winter 1969-1970
28
26
24
22
20
18
16
14
12
10
8
6
4
2
INCHES
O
N
D
J
F
M
A
M
TIME (in months)

Figure 61

Figure 62. Five day maximum, minimum and mean temperature experienced by the *Wyeomyia smithii* larvae and pupae October 1, 1969 to October 18, 1970. The effect of snow cover in minimizing the extremes in temperature throughout the winter is clearly demonstrated.

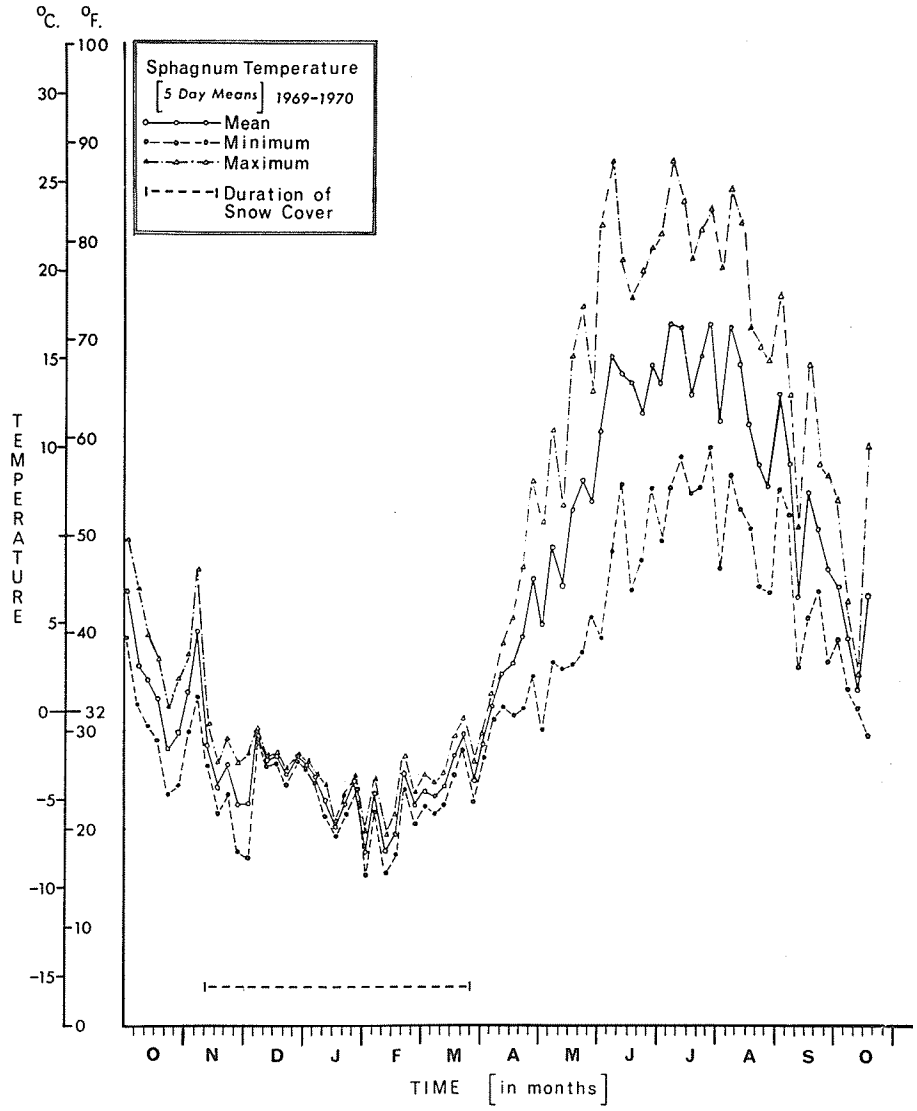

°C. °F.
Sphagnum Temperature
[5 Day Means] 1969-1970
Mean
Minimum
Maximum
Duration of Snow Cover
TEMPERATURE
TIME [in months]
O N D J F M A M J J A S O

Figure 62

Figure 63. *Wyeomyia smithii* eggs (X40) (A) infertile egg; (B) fertile egg. Visible though the chorion is the developing embryo. The head (H) is located at the blunt end (anterior) of the egg. The thorax and abdomen (T, Ab) occupy the posterior two-thirds.

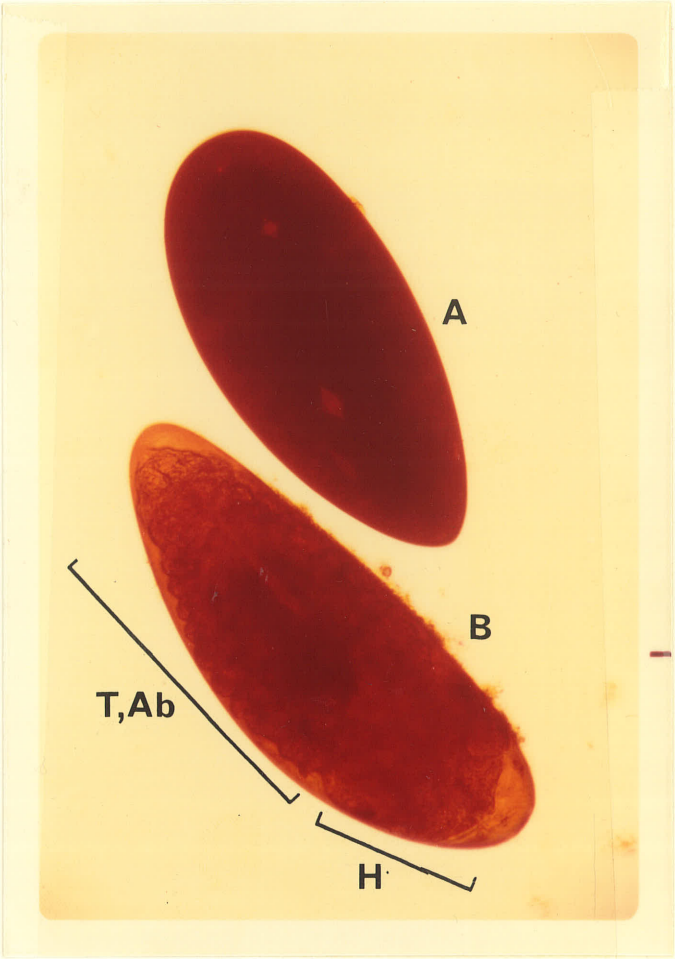


Figure 63

Figure 64. Newly opened leaf of *Sarracenia purpurea* (less than 48 hours). An opening of this size (1/4") is sufficient to allow an adult female to enter.

Figure 65. Cross section of a leaf of *Sarracenia purpurea* illustrating the zone in which eggs were often found. Dark spots (arrow) are *Wyeomyia smithii* eggs.

Figure 64

Figure 65

Figure 66. Eggs of *Wyeomyia smithii* lodged in the spines or hairs in zone four of the leaf.

Figure 67. Eggs of *Wyeomyia smithii* floating on the surface of the fluid in a young *Sarracenia purpurea* leaf.

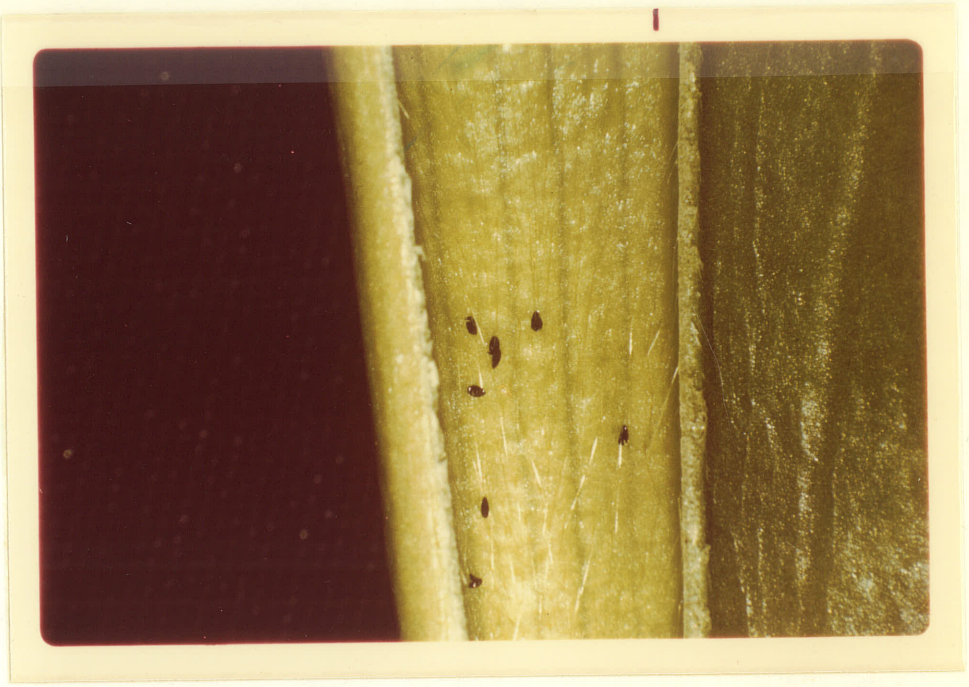


Figure 66

Figure 67

Figure 68. Head of a fourth instar *Wyeomyia smithii* larva showing location of labral mouth brushes (Lb), maxillae (M), mandibles (Ma), and esophagus (E).

Figure 69. Enlargement of the labral mouth brushes of *Wyeomyia smithii*. Both serrated (S) and unserrated (U) mouth brushes are present.

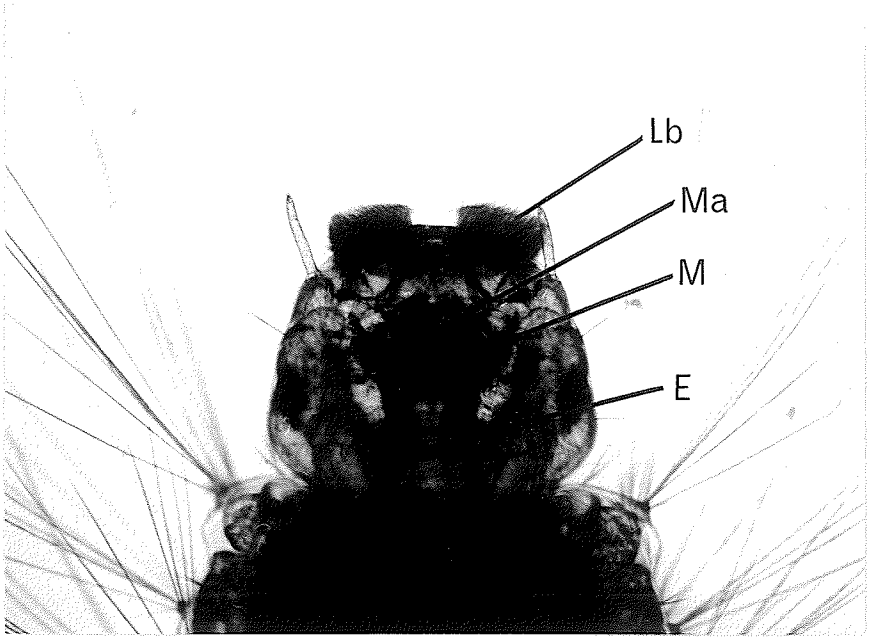


Figure 68

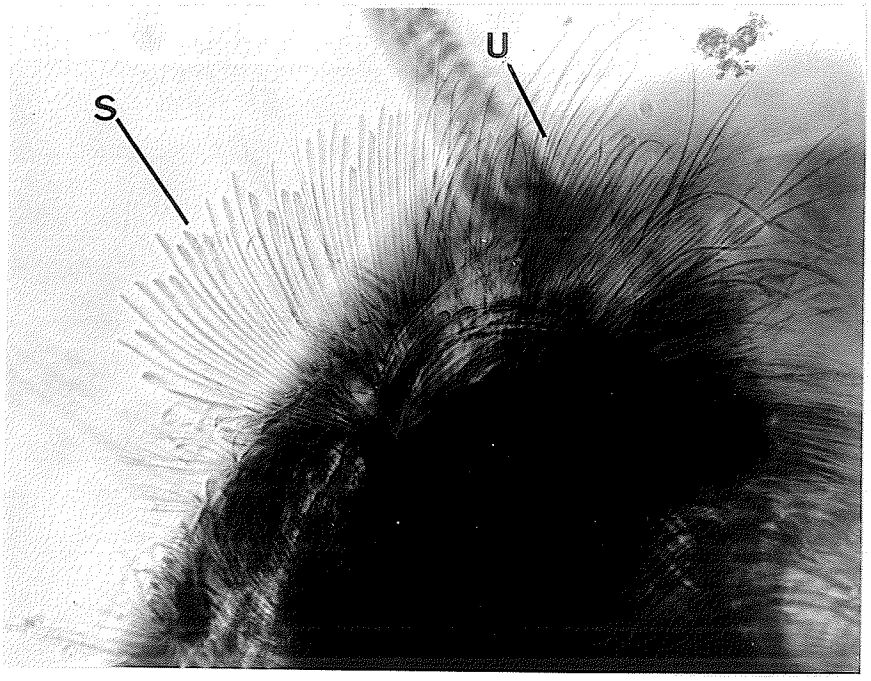


Figure 69

Figure 70. *Wyeomyia smithii* third instar larva (arrow) as they occur encased in the ice cores in the leaves of *Sarracenia purpurea*. Larvae are normally found in this curled position just above the detritis of the leaf.

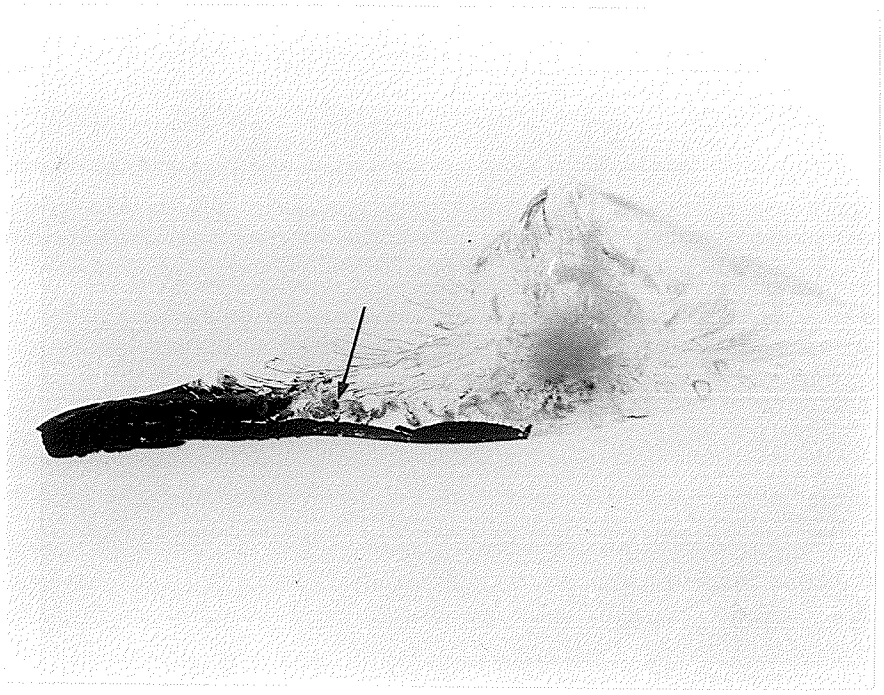


Figure 70

Figure 71. *Wyeomyia smithii* adults resting in zone one of a new *Sarracenia purpurea* leaf. This is where most adults were found.

Figure 72. A *Wyeomyia smithii* adult at rest on a small branch.

Figure 71

Figure 72

Figure 73. An adult *Wyeomyia smithii* (arrow) hovering within the mouth of a newly opened *Sarracenia purpurea* leaf.

Figure 73

Figure 74. 16 mm. sequence illustrating the hovering flight of an adult *Wyeomyia smithii* over the mouth of a pitcher leaf in the field (Pinawa Bog).

Figure 75. 16 mm. sequence illustrating the duplication of this hover flight behavior by an adult *Wyeomyia smithii* over glass vial (artificial pitcher) in the laboratory.

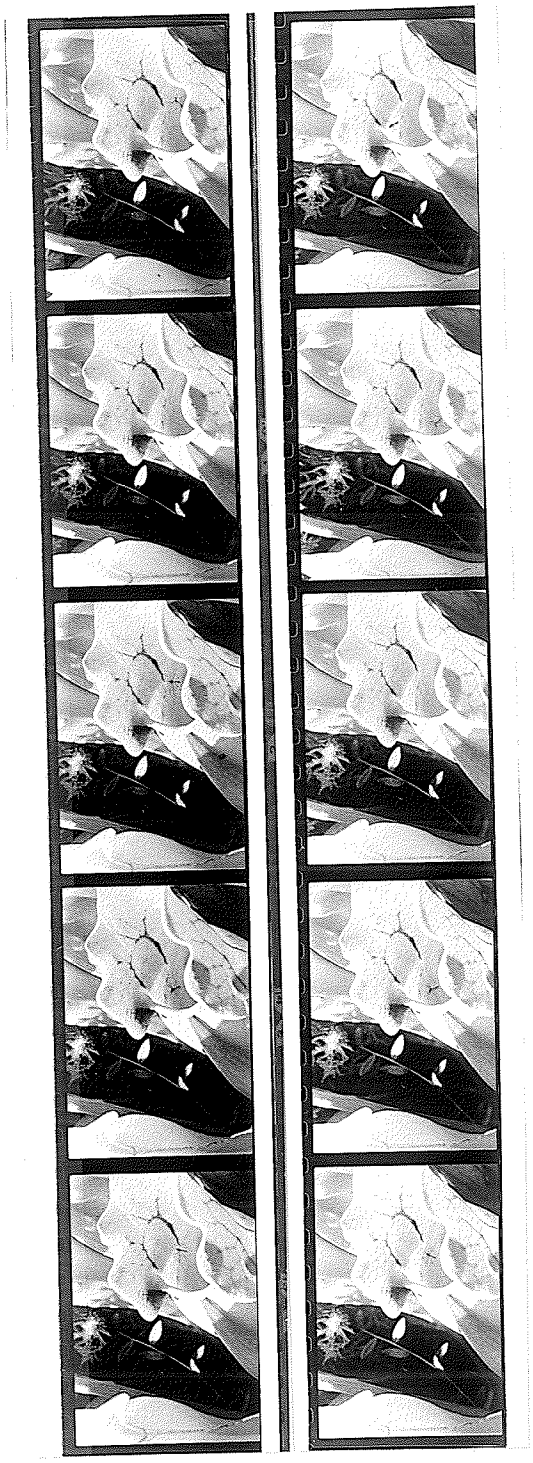


Figure 74

Figure 75

Figure 76. An adult *Wyeomyia smithii* (arrow) resting in the mouth of an artificial pitcher (glass vial) at the Telford Bog.

Figure 76

Figure 77. Complete ovaries of a newly emerged (12 hours), unfed female *Wyeomyia smithii*. Follicles are uniformly developed to stage IIIa-IIIb.

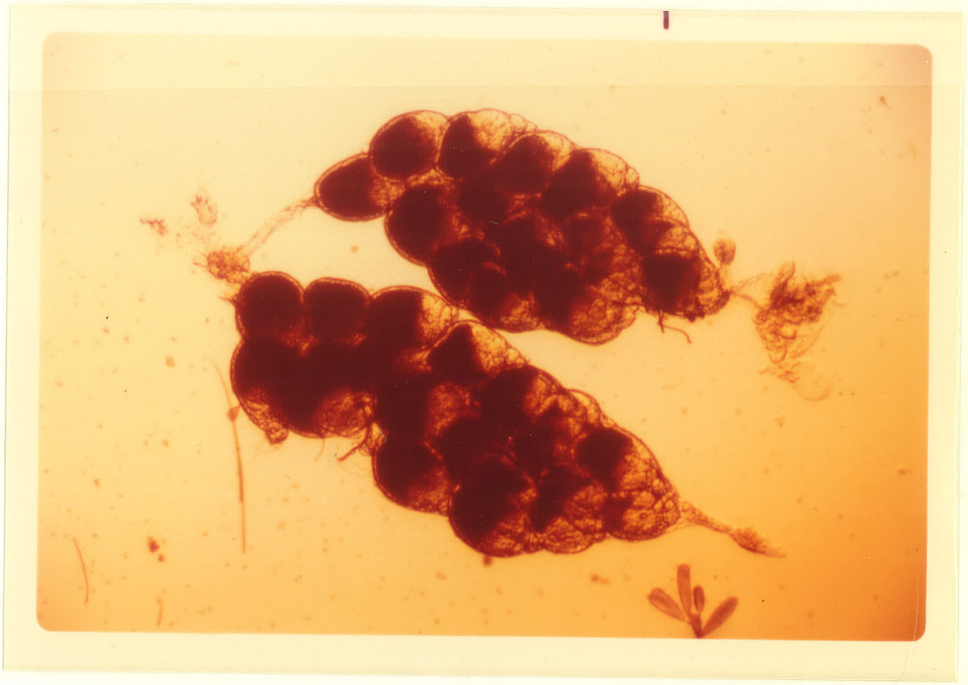


Figure 77

Figure 78. Stage IIIa follicle of an unfed female, six hours after emergence. Oocyte cytoplasm is clouded with yolk granules, obscuring the oocyte. Nurse cells are still visible. Secondary follicle is at Stage Ia-Ib.

Figure 79. Stage IIIa-IIIb follicle of an unfed female twelve hours after emergence. Yolk occupies half of the follicle. Secondary follicle is at Stage Ib.

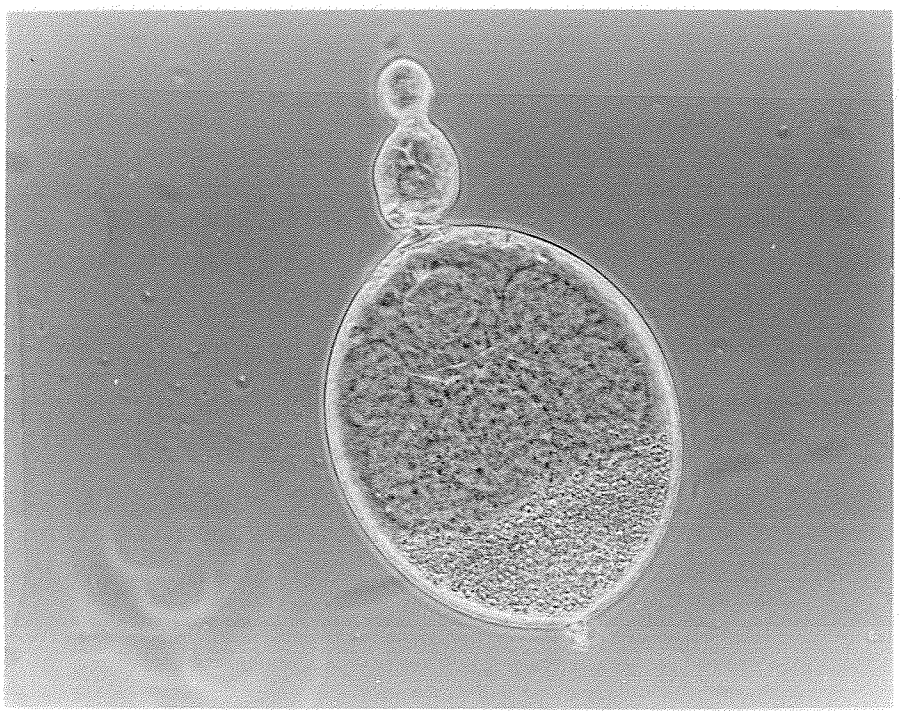


Figure 78

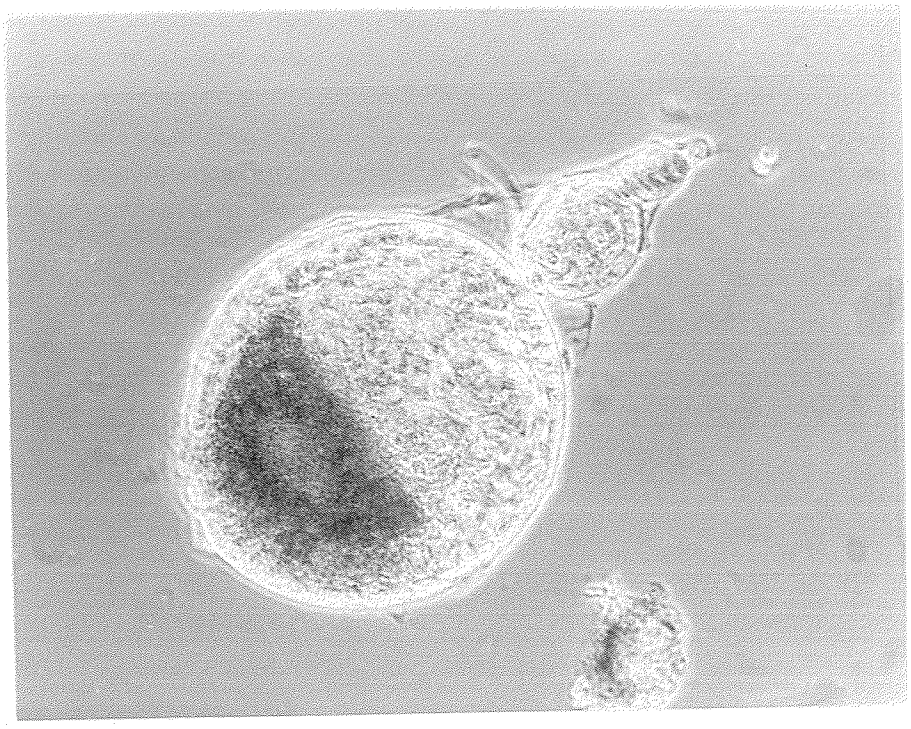


Figure 79

Figure 80. Stage IIIb follicle of an unfed female twenty-four hours after emergence. Yolk occupies two-thirds to three-quarters of the follicle. Secondary follicle is at stage Ib-IIa.

Figure 81. Stage IVa follicle of an unfed female forty-eight hours after emergence. Yolk occupies the 9/10 of the follicle, the nurse cells only 1/10. Follicle is beginning to elongate. Secondary follicle is at Stage IIa.

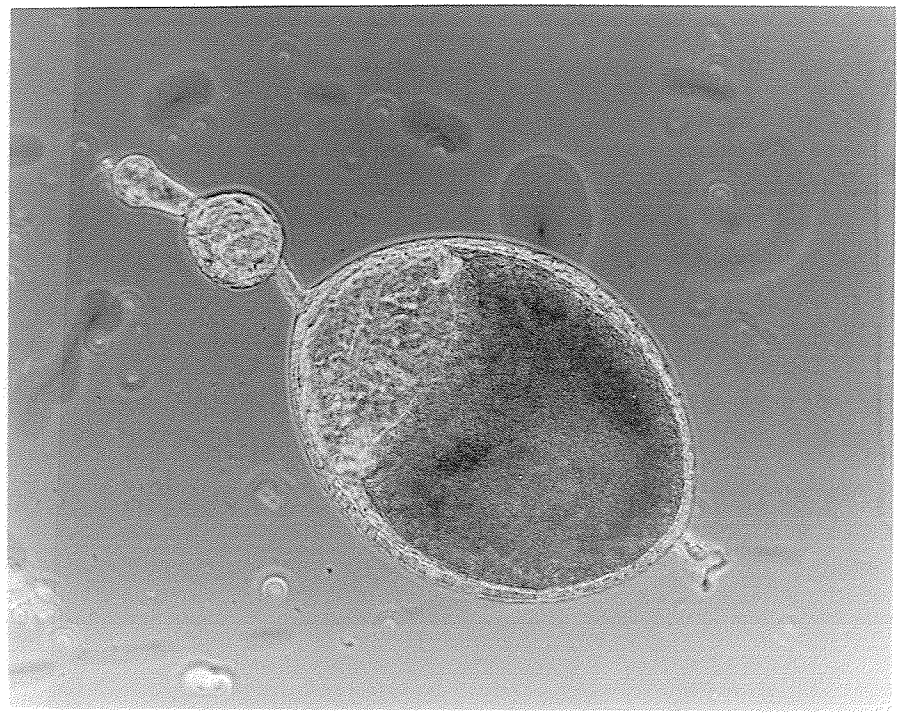


Figure 80

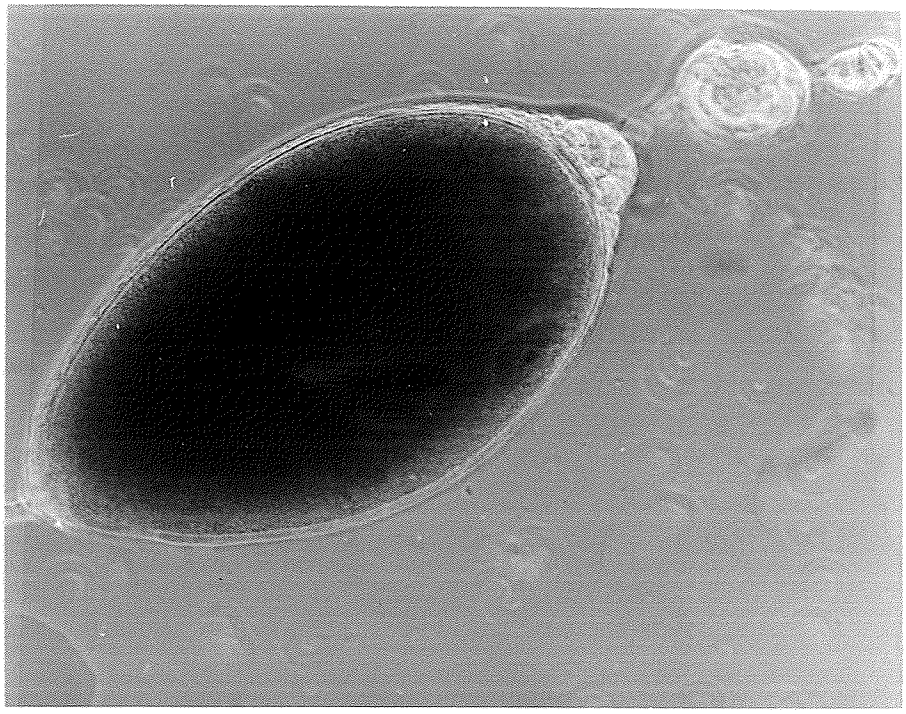


Figure 81

Figure 82. Stage IVb follicle of an unfed female seventy-two hours after emergence. Follicle begins to assume the shape of the mature egg. Secondary follicle is at Stage IIa-IIb.

Figure 83. Stage V follicle of an unfed female ninety-six hours after emergence. Follicle now has the shape of a mature egg and the chorion is beginning to form. Secondary follicle is still at Stage IIa-IIb.

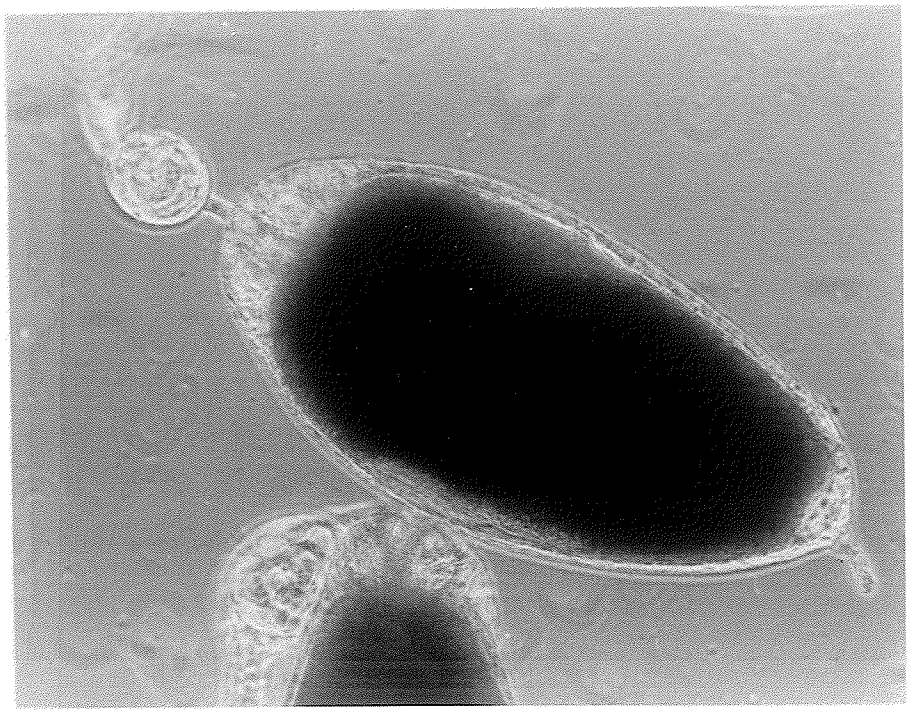


Figure 82

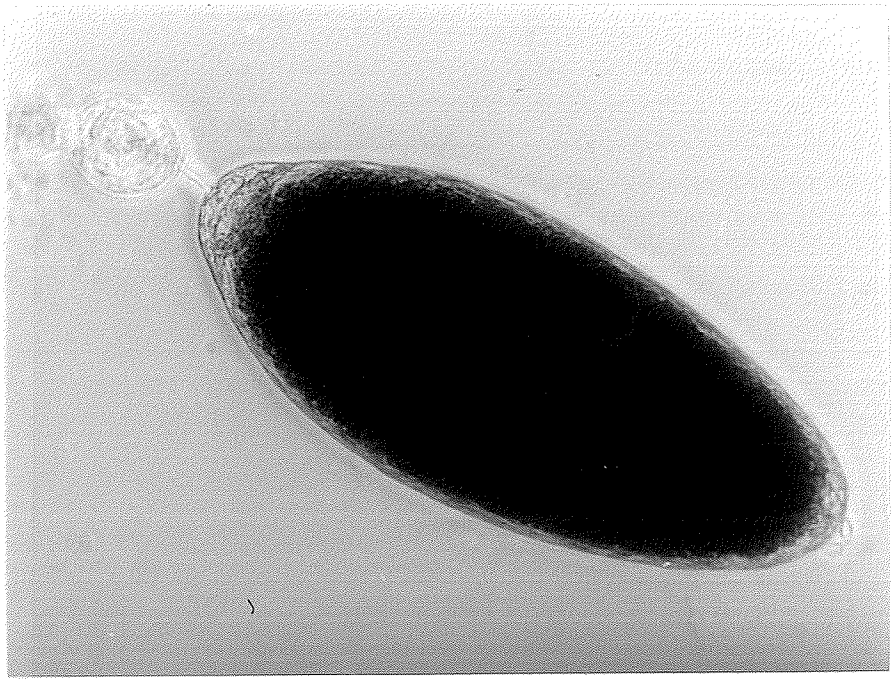


Figure 83

Figure 84. Ovary of twenty-four to thirty-six hour old female. Follicles have developed to Stage IIIb. Reabsorption of some follicles has occurred (arrow) as noted by the absence or fewer yolk granules and paler color.

Figure 88. A single follicle in which the yolk granules have been partially reabsorbed.

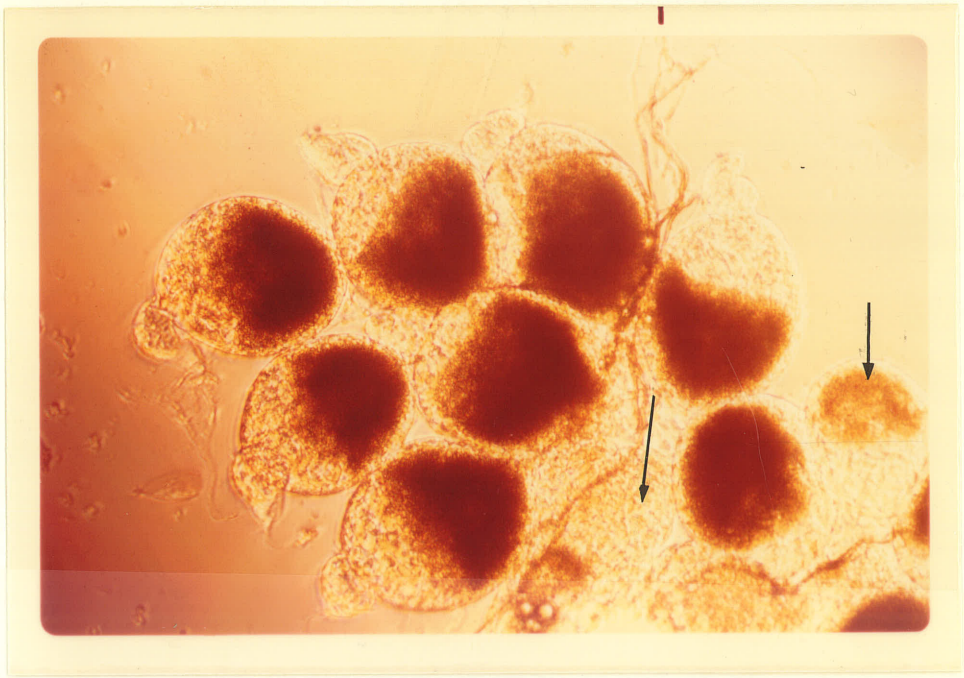


Figure 84

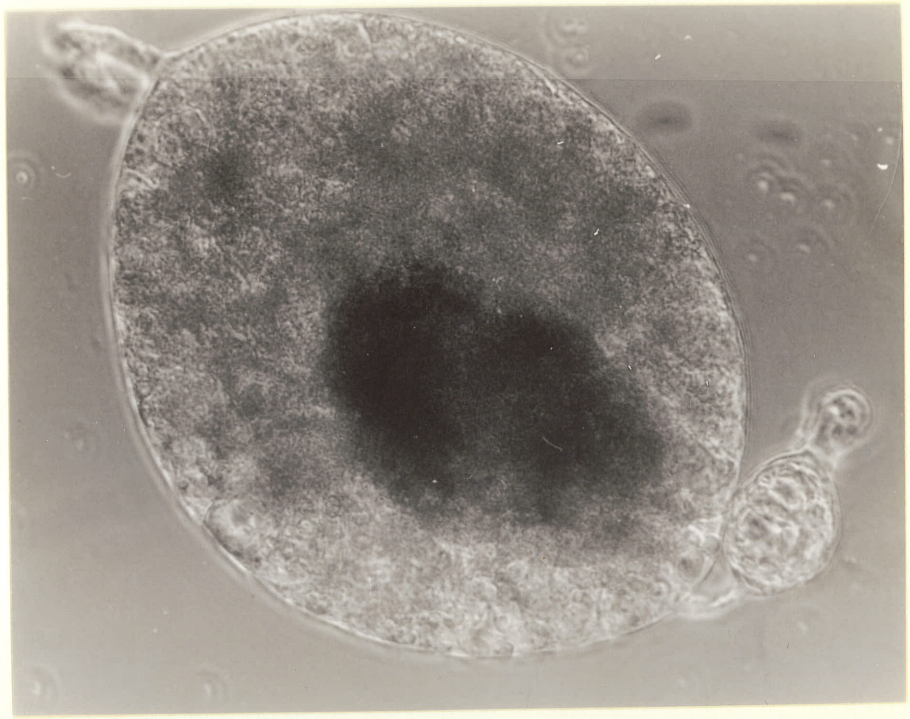


Figure 85

Figure 86. Single follicle of a newly emerged unfed female (24 hours). Primary follicle is at Stage IIIb. Secondary follicle has progressed to Stage IIIa, although it is considerably smaller than a normal IIIa primary follicle.

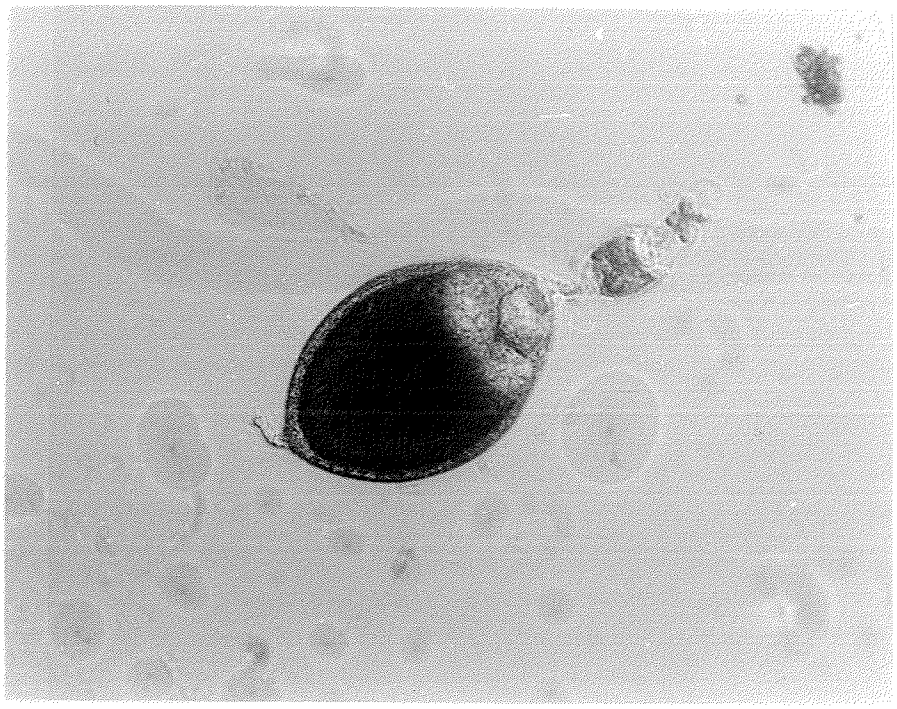


Figure 86

Figure 87. Seasonal occurrence of the various life stages of *Wyeomyia smithii* in the Pinawa Bog, 1969.

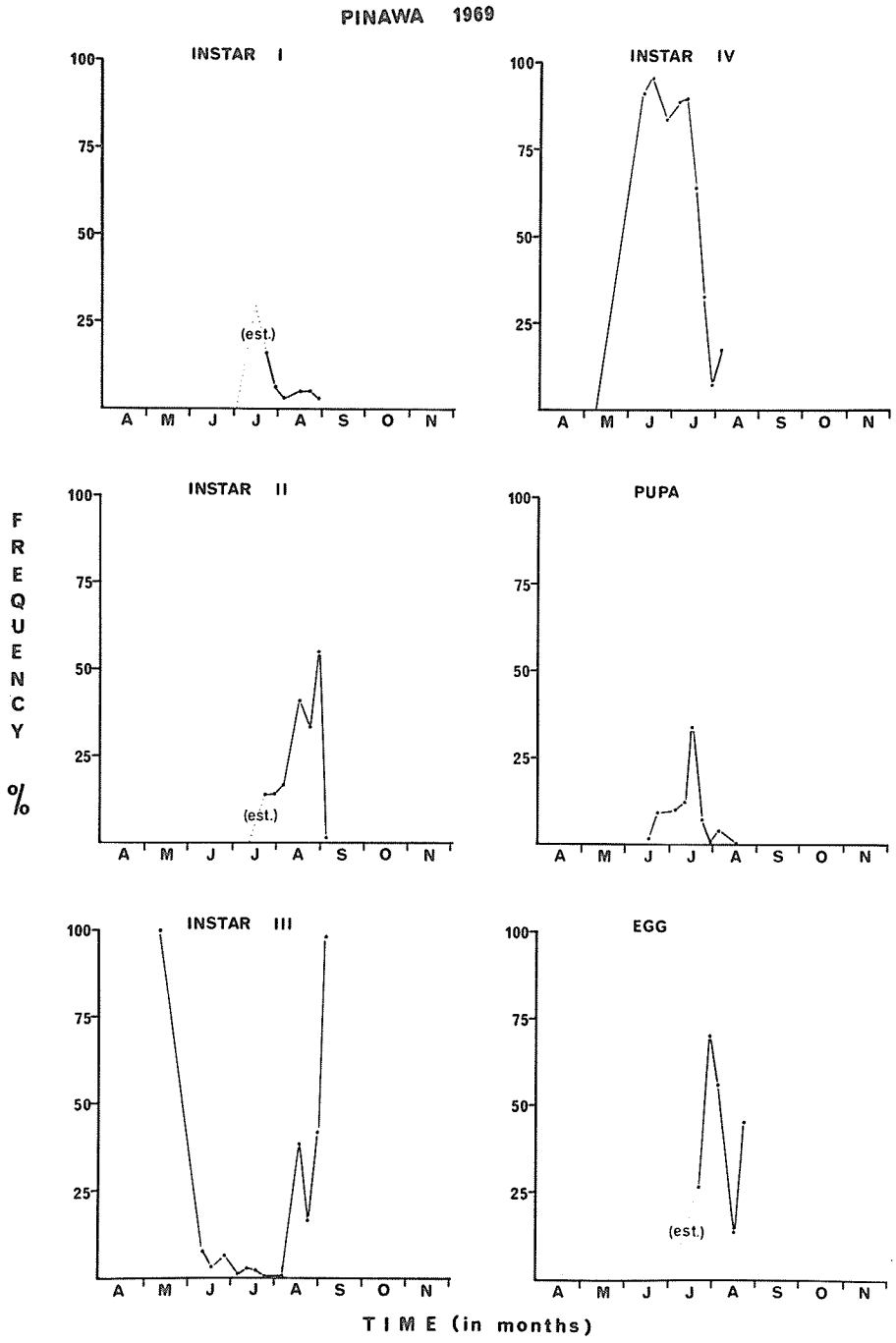

PINAWA 1969
INSTAR I
INSTAR IV
INSTAR II
PUPA
INSTAR III
EGG
(est.)
100
75
50
25
A M J J A S O N
FREQUENCY %
TIME (in months)

Figure 87

Figure 88. Seasonal occurrence of the various life stages of *Wyeomyia smithii* in the Pinawa Bog, 1970.

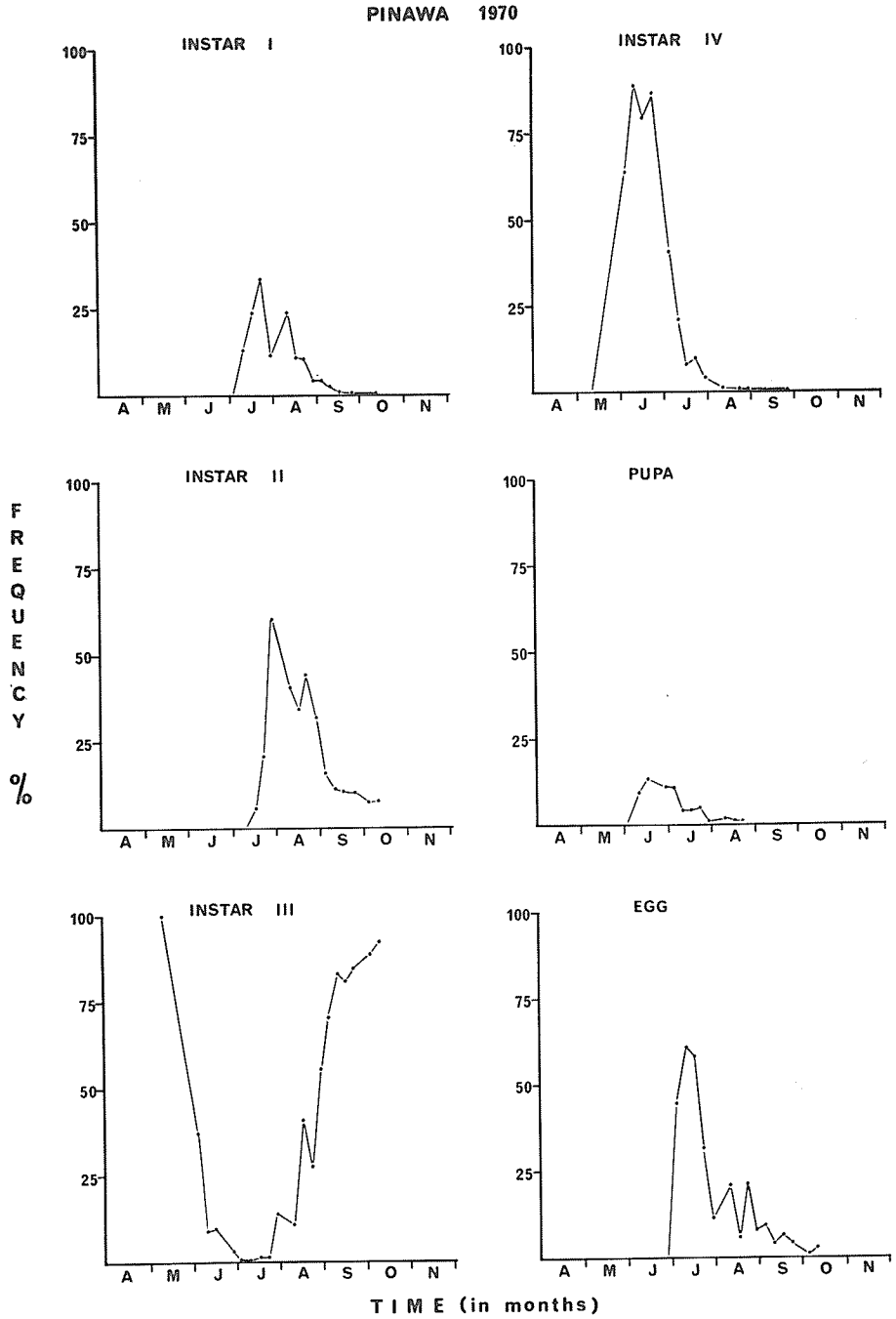

PINAWA 1970
INSTAR I
INSTAR IV
INSTAR II
PUPA
INSTAR III
EGG
100
75
50
25
A M J J A S O N
FREQUENCY %
TIME (in months)

Figure 88

Figure 89. Seasonal occurrences of the various life stages of *Wyeomyia smithii* in the Kenora Bog, 1969.

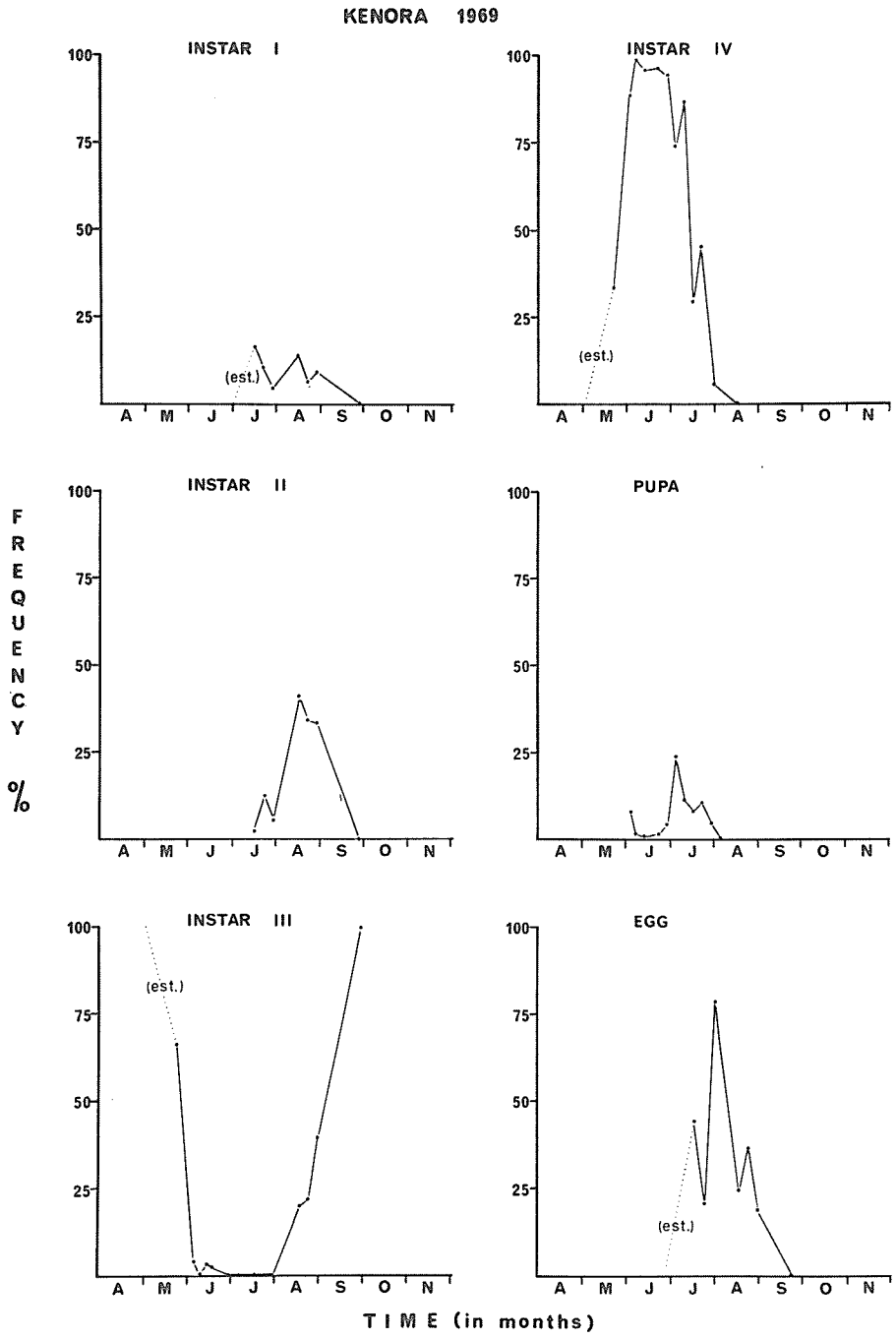

KENORA 1969
INSTAR I
INSTAR IV
INSTAR II
PUPA
INSTAR III
EGG
(est.)
100
75
50
25
A M J J A S O N
FREQUENCY %
TIME (in months)

Figure 89

Figure 90. Seasonal occurrence of the various life stages of *Wyeomyia smithii* in the Telford Bog, 1969.

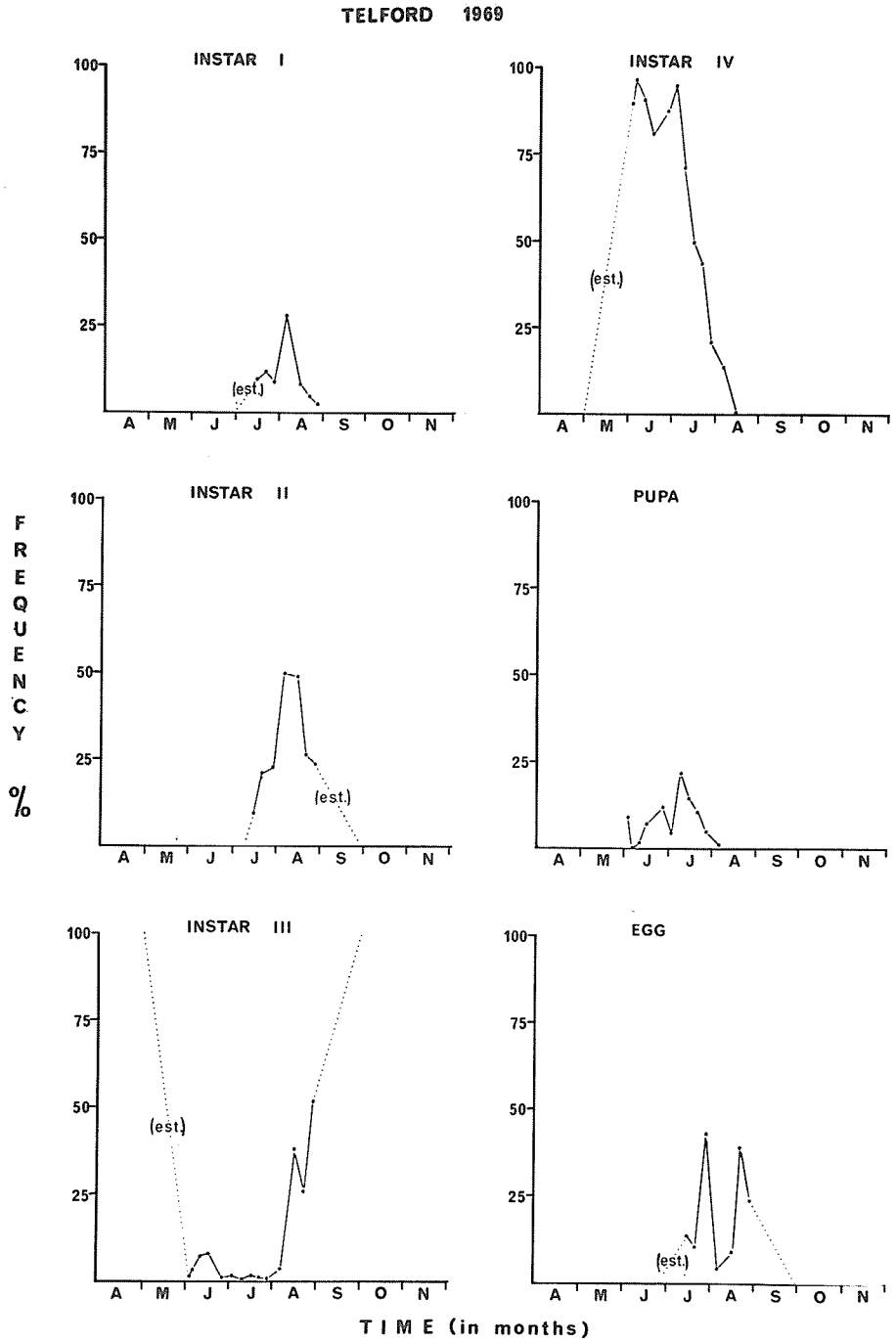

TELFORD 1969
INSTAR I
INSTAR IV
INSTAR II
PUPA
INSTAR III
EGG
100
75
50
25
(est.)
A M J J A S O N
FREQUENCY %
TIME (in months)

Figure 90

Figure 91. Annual duration of life stages of *Wyeomyia smithii*.

Duration of life stages
of Wyeomyia smithii
1 - overwintered pop^{n}.
2 - current pop^{n}.

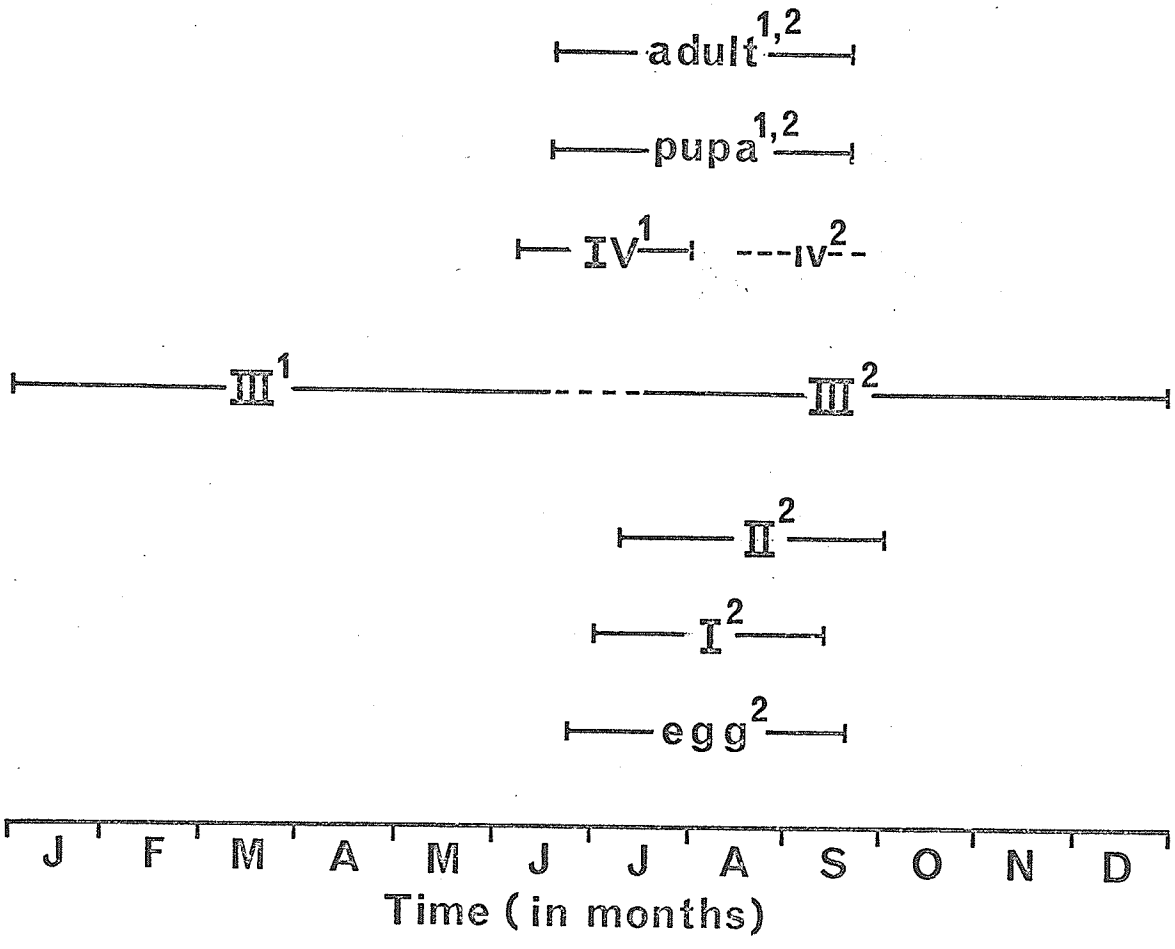
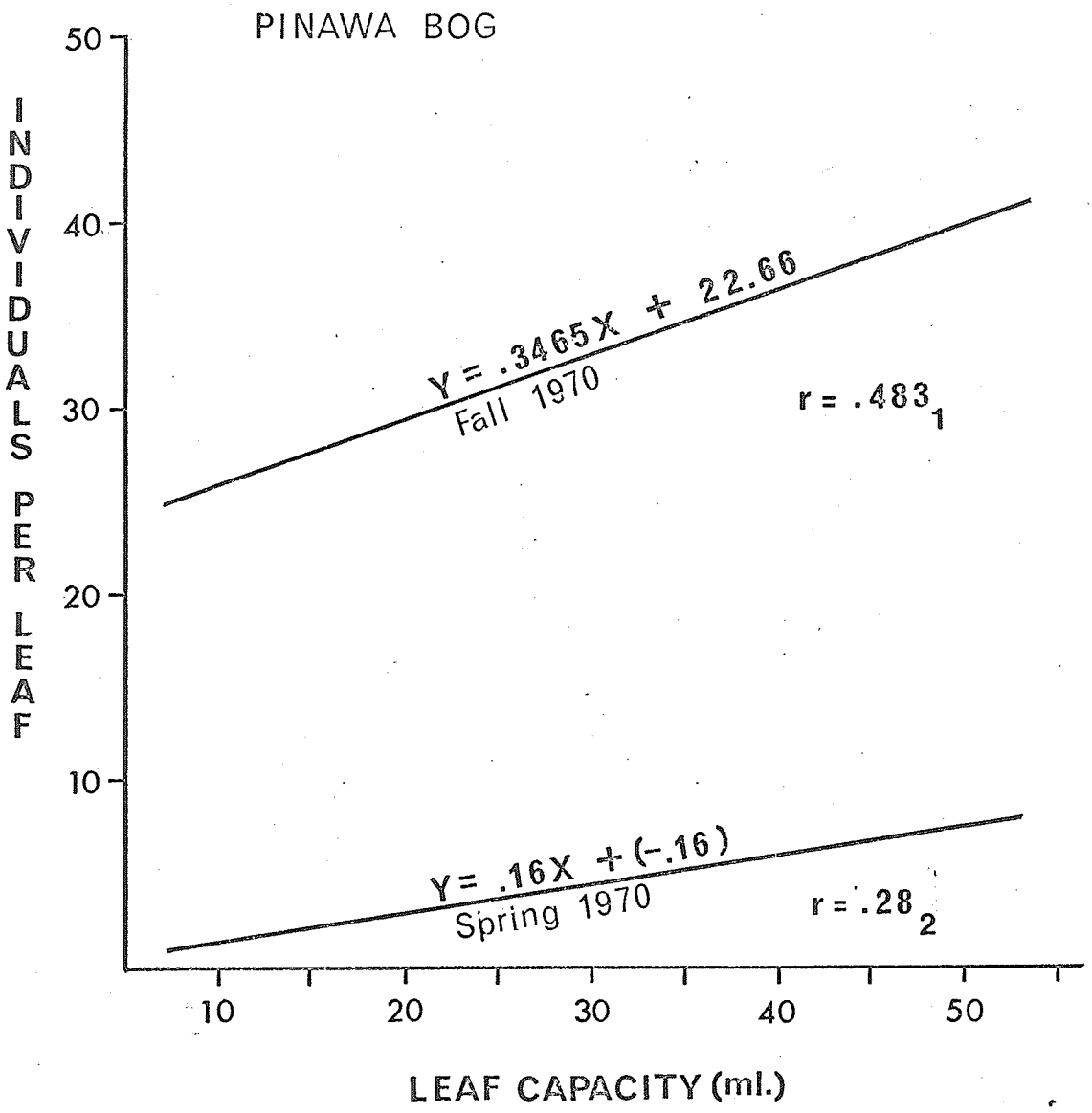


Figure 91

Figure 92. Relationship of leaf populations to leaf size based on samples taken in the spring and fall of 1970 in the Pinawa Bog.



1. SIGNIFICANT TO 1% – N-2 = 206 (SNEDECOR / 1937)
2 SIGNIFICANT TO 5% – N-2 = 104 (SNEDECOR/1937)

Figure 92

Figure 93. Annual change in mean number per leaf from old leaves (previous year's growth) to new leaves (current year's growth.

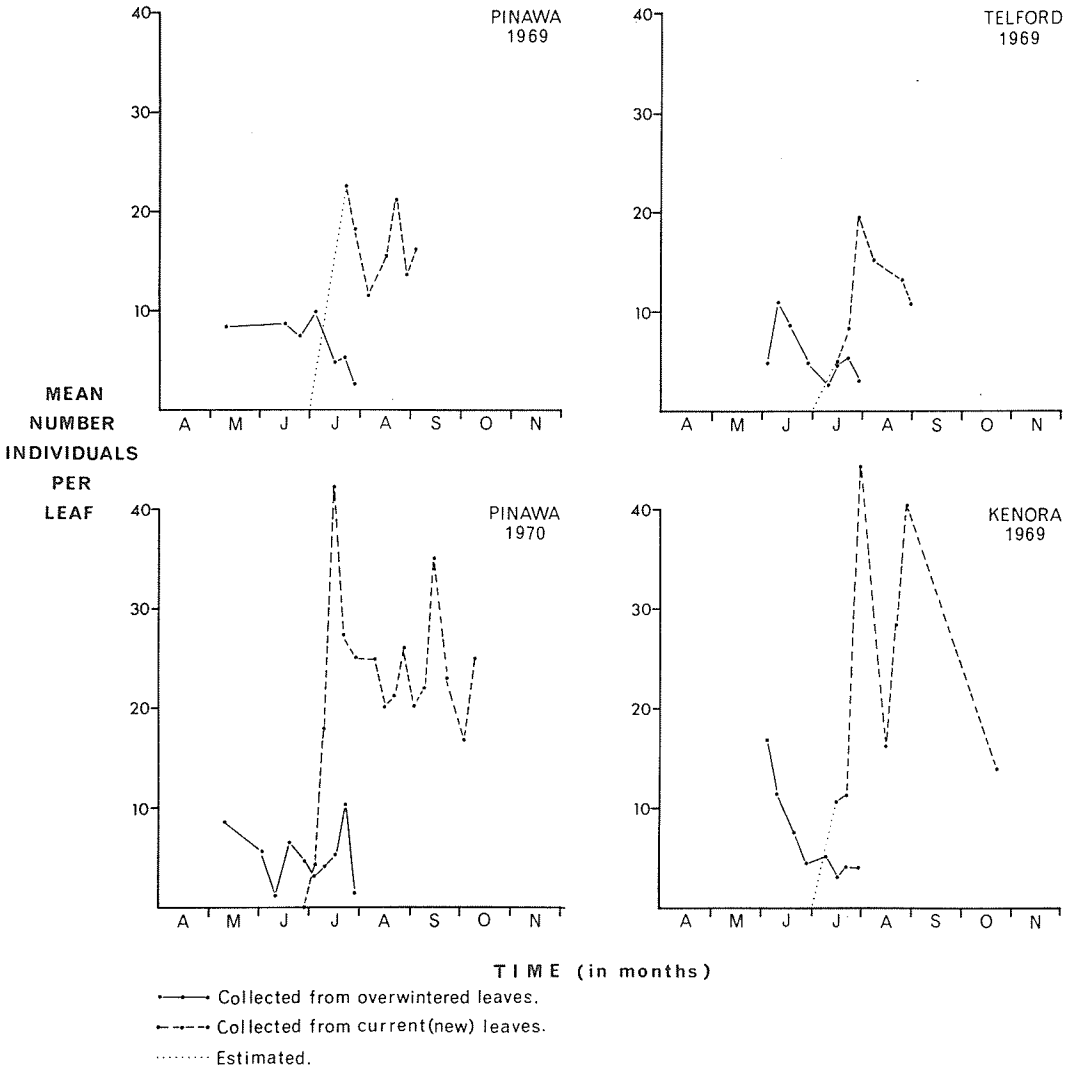

PINAWA
1969
TELFORD
1969
PINAWA
1970
KENORA
1969
MEAN
NUMBER
INDIVIDUALS
PER
LEAF
40
30
20
10
A M J J A S O N
TIME (in months)
Collected from overwintered leaves.
Collected from current(new) leaves.
Estimated.

Figure 93

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