ASPECTS OF THE REPRODUCTIVE BIOLOGY OF *Clintonia borealis* (Ait.) Raf.

by

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Foreword

This research represents two years of investigation into certain aspects of the reproductive biology of Clintonia borealis (Ait.) Raf. It covers areas that have to date remained unexplored while at the same time pursuing avenues of inquiry initiated by previous authors.

As is the case with most scientific studies, answers simply lead to more questions and it becomes beyond the capabilities of a single investigator to study them all. It is therefore the author's sincere hope that others will take up where I have left off in the investigation of this most interesting woodland plant.

Abstract

The rhizome of Clintonia borealis (Ait.) Raf. was shown to store large quantities of total nonstructural carbohydrates up until fall dormancy and to draw upon these reserves during the spring growth period, however the level of decline and rate of decline are not necessarily the same from year to year. Older rhizome segments participate in TNC storage, demonstrating high levels in the fall and low levels in the spring. In addition, roots are also capable of storing TNC and probably provide an important secondary reserve.

For a typical population in Northwestern Ontario, 3-leaved specimens were the most important members since they provided the greatest contribution towards the total population as well as the most flowering individuals. Plants with high leaf numbers produced the most rhizomes and were the ones most likely to be fertile. Population makeup, with respect to the number of plants in each leaf number category and the percentage of individuals in flower remains relatively constant from year to year for populations growing in a stable environment.

Leaf number is determined in the fall by the number of preformed leaves present in the rhizome bud. Leaves which do not reach this level of development, i.e., primordial leaves, abort the following spring. Similarly an inflorescence in the bud must have matured enough to possess a well developed stipe before the onset of dormancy, otherwise it too will abort in the spring.

Plants growing in open sites are most likely to be fertile. This phenomenon may be related to TNC storage since plants growing in the open are probably the most active photosynthetically and in turn producing the most TNC. A minimum or threshold level of TNC for inflorescence production in C. borealis is suggested.

Insect mediated cross pollination is the principal pollination mechanism in Clintonia borealis; however, the species still possesses a capacity for self pollination.

A distinct correlation exists between berry volume and the number of mature seeds contained. This is interpreted as a reproductive strategy allowing maximum seed dispersal by animal vectors since the most attractive fruit contain the greatest number of seeds.

Introduction

Clintonia borealis (Ait.) Raf. is one of five species of north temperate perennial herbs belonging to the monocot family Liliaceae. The other four species are *Clintonia andrewsiana* Torrey, *Clintonia umbellulata* (Michx.) Morong, *Clintonia uniflora* (Schult.) Kunth, and *Clintonia udensis* Trautv. & Mey. Four of the five species occur in North America; *C. borealis* and *C. umbellulata* in the east, *C. andrewsiana* and *C. uniflora* in the west. *C. udensis* is the only Asian representative of the genus. *C. andrewsiana* and *C. umbellulata* have a somewhat restricted distribution when compared with the more widespread *C. borealis* and *C. uniflora*.

The range of *C. borealis* extends from southeastern Manitoba to Newfoundland and the Maritimes in Canada and as far south as Georgia in the U.S., where it is restricted to the mountains. It is also widespread in the northern and northeastern states. Specimens have been collected as far north as Sandy Lake in Ontario and at even higher latitudes in Quebec and Labrador.

C. borealis is an inhabitant of cool woods. LaRoi (1967) has shown it to be a prominent member of the ground flora in white sprucebalsam fir stands and black spruce stands in the Canadian boreal forest, where its presence was 50% and 58% respectively. Curtis (1959) assigns a presence value of 95% and an average frequency of 31.7% to _C_. _borealis_ in the ground layer vegetation of the boreal forest in Wisconsin. In New Brunswick forests, Maclean and Wein (1977) have indicated a frequency of 58% for _C_. _borealis_ in young mixed hardwood stands with crown cover of 68%, whereas similar-aged stands with crown cover of only 5 to 22% show no sign of _Clintonia_.

_C_. _borealis_ is a small herb with two to five broad basal leaves and a leafless stalk bearing several yellowish-green bell-shaped flowers at its distal end. An individual in flower may reach a height of 40 cm but not all individuals flower yearly. The fruit is a deep blue berry containing several seeds. Gunther (1972), studying the phenodynamics of _C_. _borealis_ concluded that seed dormancy depends to some extent on chemical inhibitors accumulating in the berries and the extent of seed dormancy depends on the length of time that seeds reside in ripening berries.

Vegetative propagation occurs by means of shallow underground rhizomes and yearly growth increments are small. During the growing season, rhizome extension occurs and culminates in the fall with the production of a bud comprised either of leaves or leaves plus a primordial inflorescence. The bud is enclosed in a bud sheath which protrudes slightly above ground level. Growth of leaves and flowers from the rhizome bud meristem occurs once; subsequent new growth takes place only in the most recently produced buds. According to Gunther, perennating buds may pass through three phases of vernalization which increase the rate of bud sprouting. Utech (1973) in a biosystematic study of the genus *Clintonia* correlated the wide range of *Clintonia borealis* (along with *C. udensis* and *C. uniflora*) with their rhizome morphology. These species all possess long thin rhizomes as compared to the short thick rhizomes of *C. andrewsiana* and *C. umbellulata*. The same author also attributed present distributions to bird dispersal and ecological tolerances.

The cytology of *C. borealis* was examined by Utech and Thein (1973). The chromosome base number of the genus is x=14. Plants of *C. borealis* have chromosome numbers of 2n=28 or 2n=32 with many meiotic irregularities. The three populations examined with a count of 2n=32 were found at higher elevations of eastern North America. In a more recent paper Utech (1975) states that "given the unvaried 2n=28 number prevalent throughout the genus, and *C. borealis* in particular, it seems likely that the 2n=32 cytotype constitutes a recent evolutionary event in which the number has risen, rather than a relictual population of an ancient x=16 *Clintonia*."

TNC FIELD STUDIES

Nonstructural carbohydrates are products of photosynthesis that play an important role in the reproductive biology of perennial plants. As the term implies, nonstructural carbohydrates are not principal components of the plant body, as are cellulose and hemicellulose, but instead are substances stored in various plant organs, particularly perennating organs (rhizomes, bulbs, tubers, etc.), that are used as a ready source of energy.

The term total nonstructural carbohydrates (TNC) refers to the sum of the sugar, starch and fructosan components of nonstructural carbohydrates and can be quantitatively expressed as a percentage of the plant or plant organ's own dry weight. Sometimes referred to as total available carbohydrates (TAC) (Donart and Cook, 1969), it has been suggested that this could cause confusion among animal scientists since ruminant animals are capable of utilizing some of the structural carbohydrates (Smith, 1969). TNC is thus considered the preferred term and, as such, is used exclusively throughout this work.

Determinations of total nonstructural carbohydrates is felt to yield more useful information, from a plant management standpoint, than estimating the fraction of each individual component (Smith, 1969), since the investigator can pinpoint the periods during which energy is either readily available or not available to the plant under consideration. Using the information gathered on TNC content, control measures can be developed which, as an example, can rid an area of an undesirable species, by perhaps harvesting while TNC reserves are at a minimum, or on the other hand, promote the growth of desirable forage crops by limiting grazing while TNC reserves are low.

The TNC content of the underground portion of a perennial woodland herb, in this case the rhizome of *Clintonia borealis*, was expected to follow a seasonal cycle of storage and utilization. Information gathered about this cycle would be useful in understanding more about the reproductive biology of the species. This is a significant area of the biology of temperate herbaceous plants that has received little attention from investigators.

METHODS

A small site on Lakehead University campus, measuring approximately 200 square meters, was selected for study during the spring of 1978, in which an adequate supply of *Clintonia borealis*, for TNC determinations, would be guaranteed. Specimens of *Populus tremuloides* Michx. comprised the dominant woody species on the site together with scattered representatives of *Prunus pensylvanica* L. f. and *Cornus stolonifera* Michx. Besides *Clintonia borealis*, the most common herbaceous plants were *Aster macrophyllus* L., *Aralia nudicaulis* L. and *Streptopus roseus* Michx. The soil in this area was basically sandy with a well developed humus layer and good drainage. No appreciable slope existed in any direction.

In order to maintain a certain degree of consistency between samples and reduce, as much as possible, fluctuations in TNC levels due to obvious differences between specimens, such as leaf number and presence or absence of flowers, only three-leaved, nonflowering specimens were collected.

Leaf expansion was complete about one week following the start of collecting in 1978; however in 1979 collecting began prior to expansion and therefore it was decided to monitor the progress of plant growth by measuring the length of the first and third leaves of 25 randomly selected plants located at the time of each collection.

For TNC determinations, a sample consisting of five plants, selected at random, was dug up using a hand trowel and brought to the laboratory for preparation. Table 1 lists the dates upon which collections were made.

During 1978, that portion of the rhizome produced in 1977 was retained, while in 1979 the 1978 portion was used. The samples taken on May 26 and November 1, 1978 included rhizome increments to 1974. These were also retained and analyzed to gather data on TNC levels present in the older segments of the rhizome at both the beginning and end of the growing season.

Since the rhizome was the organ of interest, all other portions of the plant were severed and discarded. Each rhizome was carefully washed in cool running water and, at the same time, the epidermis was scraped off. The rhizomes were then placed in the bottom of a glass Petri dish in a convection type oven, preset at 90° C, for one hour. The initial high drying temperature was necessary to halt the activity of any respiratory enzymes that might have reduced the levels of TNC through their activity. Following this period, the oven temperature was reduced to 60° C, at which the rhizomes were brought to complete dryness. The method of preparation of samples and also the procedure for analysis of TNC was developed by Smith (1969).

The analysis for TNC can be separated into two parts: first, the removal of total nonstructural carbohydrates from the dried material by an enzyme solution which breaks them down into monomers; and second, the analysis of the resulting solution for reducing power which yields a result expressed as percent TNC on a dry weight basis.

Briefly the procedure is as follows (see Table 2): An accurately weighed sample was boiled in a small amount of water to gelatinize starches, and then incubated in a buffered α-amylase solution at 38° for 44 hours. The solution was then filtered, centrifuged, refrigerated, refiltered and an aliquot analyzed for reducing power.

RESULTS

Table 3 lists the results of the analysis for total nonstructural carbohydrate content opposite the date of collection of rhizomes. The quantities are expressed as per cent total nonstructural carbohydrates on a dry weight basis.

On May 26, 1978, the date of first sampling, TNC reserves in the 1977 rhizome were calculated at 18.2 per cent. The low for 1978 was reached on or about June 2 at 13.8 per cent. From this point on, recovery of reserves was rapid with a distinct plateau of about 37 per cent reached around June 26th that continued throughout July and August. By November 1, TNC reserves had declined to 31.9 per cent in the 1977 portion, while in the newly formed 1978 increment they were 30.8 per cent.

TNC content was 29.3 per cent on May 8, the date of first collection in 1979. By May 17 reserves had declined to 23.2 per cent but by May 24, reserves had increased to 27.6 per cent, and continued to do so consistently into June, being 28 per cent on June 4 and 31.6 per cent on June 11.

Table 4 is a comparison of TNC reserves in the rhizome with average leaf length of plants measured on the same day of collections made during 1979. The decline in reserves on May 17 corresponds to the beginning of leaf expansion. By the time leaf expansion was complete, sometime between June 4 and June 11, reserves had increased to slightly over 30 per cent.

Beginning and end-of-season figures for TNC content of rhizome increments back to 1974 are listed in Table 5. All portions of the rhizome system examined showed relatively low levels of TNC during the early part of the growing season while the opposite situation was apparent at the end of the growing season with much higher amounts in all segments. In addition, TNC levels in the oldest portions of the rhizome showed the largest fluctuations.

TABLE 1

COLLECTION DATES OF SPECIMENS OF *Clintonia borealis* USED FOR TOTAL NONSTRUCTURAL CARBOHYDRATE DETERMINATIONS

1978	1979
May 26	May 8
	17
	24
June 2	June 4
9	11
20	
26	
July 5	
13	
21	
Aug. 2	
14	
24	
Nov. 1	

TABLE 2

AN OUTLINE OF THE METHOD OF ANALYSIS FOR TOTAL NONSTRUCTURAL CARBOHYDRATES USED ON THE RHIZOMES OF *Clintonia borealis*

REMOVING TNC

1. Weigh sample (100-500 mg)
2. Gelatinize starches in 15 ml boiling water
3. Incubate in 20 ml buffered enzyme (Clarase 900) solution (38° C for 44 hrs)
4. Filter through Whatman #1 filter paper; add 2 ml of 10% lead acetate solution
5. Centrifuge 5 mins. at ca 550 x g
6. Add ca 100 mg potassium oxalate and refrigerate (min. 4 hrs)
7. Refilter through Whatman #42

ANALYSIS FOR REDUCING POWER

To an aliquot of the sample from the above filtrate

1. Add 10 ml Reagent "50" (10% copper sulphate solution with potassium iodide & potassium oxalate added)
2. Heat in boiling water for 15 minutes
3. Cool and add 2 ml potassium iodide-potassium oxalate solution and 10 ml 1N sulphuric acid.
4. Add starch indicator and titrate with 0.02 N sodium thiosulphate.

TABLE 3

TNC CONTENT OF THE RHIZOME OF SPECIMENS *Clintonia borealis*

Date of Collection		% TNC Content
1978	May 26	18.2
	June 2	13.8
	9	23.6
	20	35.3
	26	37.1
	July 5	40.3
	13	38.4
	21	38.7
	Aug. 2	36.8
	14	37.3
	24	37.8
	Nov. 1	31.9
	1*	30.8
1979	May 8	29.3
	17	23.2
	24	27.6
	June 4	28.0
	11	31.6

* indicates 1978 rhizome increment

TABLE 4

TNC CONTENT OF RHIZOMES COMPARED TO AVERAGE LEAF LENGTH FOR *Clintonia borealis* SAMPLED DURING 1979

Date	% TNC Content	Average Length and Range of Lengths of First Leaf	Average Length and Range of Lengths of Third Leaf
May 8	29.3	----- before leaf expansion -------	
May 17	23.2	4.24 cm; 2.0 - 6.75 cm.	3.86 cm; 1.75-5.5 cm.
May 24	27.6	8.82 cm; 5.75-10.5 cm.	9.12 cm; 5.75-11.0 cm.
June 4	28.0	17.59 cm; 11.75-22.5 cm.	17.06 cm; 13.25-24.0 cm.
June 11	31.6	18.63 cm; 16.5-23.0 cm.	20.21 cm; 17.0-23.5 cm.

TABLE 5

TNC LEVELS IN THE RHIZOME INCREMENTS OF *Clintonia borealis* FOR THE YEARS 1974 TO 1978

Date of Collection	Year Increment Produced	% TNC Content
May 26, 1978	1974	14.6
"	1975	11.3
"	1976	13.6
"	1977	18.2
November 1, 1978	1974	39.9
"	1975	45.3
"	1976	32.9
"	1977	31.9
"	1978	30.8

TABLE 6

A COMPARISON BETWEEN THE TIMING, OVER TWO SEASONS, OF THREE IMPORTANT PHENOLOGICAL EVENTS IN THE LIFE CYCLE OF *Clintonia borealis*

May 16, 1978 - bud break
June 2, 1978 - leaf expansion complete (estimated)
June 3, 1978 - flowers opening

May 17, 1979 - bud break
June 11, 1979 - leaf expansion complete
June 13, 1979 - flowers opening

DISCUSSION

Results for the analysis of total nonstructural carbohydrate content in the rhizome of Clintonia borealis revealed a distinct cycle of storage and depletion of reserves. Rhizomes collected during the early growing season had a period of relatively low reserves, the plants having used them as an energy source during the spring growth spurt. During this period, when growth is quite rapid, reserves are utilized faster than they can be replenished by photosynthesis (Hadley and Bliss, 1964).

Comparison between average leaf length of the first and third leaves and TNC content demonstrate that, during 1979, rhizome reserves began being replenished very soon after leaf expansion commenced, between May 8 and 17. That initial growth spurt resulted in a decline of greater than 6 percent in TNC reserves; however, almost immediately reserves began to accumulate and, within seven days, had risen by 4.4 percent to 27.6 percent, while average leaf length for the first and third leaves had increased 108 percent and 136 percent respectively. As leaf expansion progressed, TNC reserves continued to accumulate and by June 11, when expansion was considered essentially complete, reserves had exceeded the 30 percent mark.

In contrast to 1979, a shift in the spring TNC cycle was evident during 1978. TNC levels reached much lower levels during 1978 than 1979 and reached these levels on later dates. A difference in excess of 9 per cent exists between the lowest TNC reading obtained for each year (June 2, 1978: 13.8%); May 17, 1979: 23.2%). At the same time, fifteen days separate these two dates during each year.

Table 6 provides a comparison between the timing of bud break, complete leaf expansion, and first appearance of flowers for the two years 1978 and 1979, on the study site. Once again, a shift can be demonstrated; however, this time the shift resulted in two of three major phenodynamic events occurring on significantly later dates during 1979 than 1978. While bud emergence began at the same time, complete leaf expansion, and flower opening eventually lagged behind the same events in 1978 by about ten days in 1979.

It is apparent that the spring TNC cycle is more complex than originally suspected. While the plant certainly places demands upon its TNC stores during the spring, the cycle is not inexorably tied to the period of leaf expansion. At the same time, the rate and degree of depletion of reserves are not the same from year to year.

Donart (1969) states that for perennial plants seasonal carbohydrate reserves are a general trend but that the magnitude and timing of carbohydrate low is variable and dependent upon species.

Linde *et al.* (1976) studied a population of *Typha angustifolia* L.

in Wisconsin during 1971 and 1972 and found a distinct TNC cycle in the rhizome. The decline in reserves was essentially synchronous with plant expansion, the decline beginning around the third week of April and continuing until a low was reached in the third week of June during 1972. Any minor rise in rhizome reserves was attributed to TNC being translocated from other areas of the plant. Sampling was not initiated in 1971 until about June 20; however during this year TNC reserves did not reach a low until two weeks later. The authors attributed the difference in timing between 1971 and 1972 to environmental factors, specifically water levels and temperature which shifted the plants' phenology.

The carbohydrate content of roots, rhizomes and shoots of several species of alpine tundra plants was investigated by Mooney and Billings (1960). The cyclic nature of carbohydrate stores was apparent in all plants studied but found to be more pronounced in some species than others. A generalized cycle for the alpine plants Saxifraga rhomboidea Greene, Polygonum bistortoides Pursh and Geum turbinatum (sic) indicated high carbohydrate content of underground storage organs at fall dormancy with depletion of reserves commencing prior to and immediately following snowmelt. Carbohydrate levels experienced the greatest decline during early shoot growth following which recovery of reserves was rapid.

Fluctuations in the level of TNC reserves in the rhizome of

C. borealis are due primarily to the demands of leaf expansion but are probably considerably modified by changes in microclimate, especially as these changes affect photosynthesis. A well developed overstory was observed to be in place at the time of first collection during 1978; however, the overstory was poorly developed in 1979 due to a late spring. Thus during the spring of 1979 temperature and light energy levels at ground level were likely much higher than 1978 which allowed translocation of photosynthate from growing leaves to the rhizomes much sooner. In turn this could be responsible for higher minimum reserve levels and more rapid recovery of reserves in 1979.

GROWTH CHAMBER
STUDIES

An experiment designed to monitor the response of the developing rhizome of Clintonia borealis to controlled conditions of light energy (intensity) and soil temperature was undertaken during 1978. Of interest was the amount of nonstructural carbohydrate stored by the underground portions of the plant, and whether high carbohydrate levels would result in production of an inflorescence.

Werner (1975) has found that the minimum size for rosettes of Dipsacus follonum L. must be 20 cm before flowering will occur. Frye (1977) notes that the bulb of the trout lily, Erythronium americanum Ker., must develop to a "sufficient" size before the plant will flower. Other authors, Salisbury (1963) and Hillman (1964) have reviewed the literature concerning carbohydrate involvement in flower production. While carbohydrate is not considered to be directly responsible for floral initiation, its presence is required in some plants before inductive treatments are effective.

The quantity and quality of light energy received by the plants in the field is governed primarily by composition and extent of development of the leafy portion of the overstory. Here, overstory refers to all plants that compete with Clintonia borealis for sunlight and may therefore be herbaceous, shrubby or arboreal types.

According to Coombe (1957), in summer the closed canopy of a deciduous wood results in a "green-dark red" shade; however, the closed canopy of a coniferous wood behaves more like a neutral filter, cutting down all wave lengths equally. Gaps within the canopy allow "blue" light to reach the undergrowth. Differences in the quality of light between deciduous and coniferous stands could result in different growth responses by the understory vegetation. Measurements of the quantity of sunlight present at ground level are really only meaningful if the spectral composition of that light is also considered.

Soil temperature could be a factor governing inflorescence production at the spring and summer temperature extremes encountered by the developing bud since light breaks within the overstory will result in higher soil temperatures at the point of interception as compared to temperatures in adjacent shaded areas. This, in turn, could affect TNC content within the rhizome by altering the balance between photosynthesis and respiration within the plant. Cooper (1973) states that the temperature of a root system can affect flowering by altering net assimilation rate, while Proebsting (1957) found that runner production in strawberry was more abundant at 24^{o} C than at other temperatures ranging from 7^{o}-32^{o} C.

Clintonia borealis is apparently a day-neutral plant, since specimens, in nature, growing under the same conditions, with regard to photoperiod, may or may not produce an inflorescence. For this reason the effect of varying photoperiod was not a factor in the experiment.

METHODS

The experiment was conducted using a Controlled Environments Ltd. environmental chamber. The chamber is a walk-in type measuring 85" long x 63" wide x 95" high. The plants were kept in two large wooden trays, measuring 75" long x 24" wide x 5" deep, which were fabricated from 1/2" plywood and 1" x 6" boards. At each end of the tray was a 24" wide x 30" high upright section, also constructed from 1/2" plywood, while a 24" x 27" high section positioned in the middle of each tray separated adjacent treatment groups from one another. All joints were sealed with silicone sealer and both trays painted with two coats of gray epoxy paint.

Five 24" strip fixtures were rivetted to braces to provide 6" centre to centre spacing between each one. Each lighting unit was then suspended over the tray by chains hooked onto two 76" long wooden supports which spanned the entire length of each tray and rested atop the upright plywood sections.

Drainage holes were drilled through the bottom section at one end of each tray and the opposite end elevated one inch. A one inch layer of crushed rock covered with four inches of soil (1/3 bog peat: 2/3 general soil mix, i.e., 50% sterilized sandy loam, 25% milled sphagnum, 25% perlite) was placed in each tray.

A cooling system for the soil, measuring 73" long x 22" wide, was fabricated from 1/2" diameter copper pipe and placed atop the gravel layer in one tray. The coil was connected to a cold water tap and drain using plastic tubing, and cold water was continuously circulated through the system at a temperature of between 5^o and 15^o C over the duration of the experiment. A maximum temperature rise of 1.5^o C was experienced between the incoming water and the soil adjacent to the cooling system. Soil temperature readings for a 24 hour period were taken weekly using a Heathkit recorder coupled to a telethermometer (Yellow Springs Instruments) with the probe at a depth of 3 cm.

Lighting was provided by Grolux standard lamps at a level of either 1.5 uW/cm^2/nanometer or 3 uW/cm^2/nanometer in the 400-500 (blue) and 600 to 700 nanometer (red) spectral bands. Light energy levels were measured with an International Light Inc. plant growth photometer, IL 150.

Photoperiod was a constant 16 hours light, 8 hours darkness and chamber temperature was synchronized with photoperiod at 22^o C day and 16^o C night.

Sixty, three-leaved nonflowering specimens of <u>Clintonia borealis</u> were transplanted to the growth chamber on June 5th, 1978. Each plant consisted of leaves, roots and the most recently produced rhizome increment, i.e., 1977.

Fifteen plants were allotted to each treatment and were arranged with a six inch spacing between any two plants and six inches between the edge of the tray and the nearest row of plants.

The four treatments were as follows:

Treatment 1
light energy - 3.0 uW/cm^2/nanometer (red and blue spectral bands)
soil temperature - fluctuates with ambient chamber temperature

Treatment 2
light energy - 3.0 uW/cm^2/nanometer (red and blue spectral bands)
soil temperature - always below 16.5^{o} C

Treatment 3
light energy - 1.5 uW/cm^2/nanometer (red and blue spectral bands
soil temperature - fluctuates with ambient chamber temperature

Treatment 4
light energy - 1.5 uW/cm^2/nanometer (red and blue spectral bands
soil temperature - always below 16.5^{o} C

The plants received regular waterings and one application of 20/20/20 fertilizer, at a ratio of one part concentrated fertilizer to sixteen parts water, during the third week in July.

The experiment was terminated on October 1st, 1978. At this time 55 plants remained alive. These were collected along with the rhizomes, roots and perennating buds they had produced while in the chamber. The parent plant was removed and discarded and the old rhizome and the newly produced rhizome and roots were dried and analyzed for total nonstructural carbohydrate content (see Table 2). The roots were included in the analyses because of the large amount produced by the developing rhizomes under the chamber conditions. The perennating bud was dissected and examined, using a dissecting microscope, to check for the presence of a developing inflorescence.

RESULTS

Table 7 is a summary of the results on rhizome and inflorescence production for specimens of Clintonia borealis maintained under conditions of varied soil temperatures and light energy levels.

In Treatment 1, with light energy of 3.0 uW/cm^2 and soil temperature controlled by ambient chamber temperature, 13 parent plants survived and produced 22 new rhizomes for a percent increase in the new generation of 69.2. Mean length of new rhizomes was 33 mm with a range from 11 to 50 mm. The number of rhizome buds with flower primordia was 21 while one had none.

In Treatment 2, with light energy at 3.0 uW/cm^2 and soil temperature always below 16.5^o C, 13 parent plants survived and produced 21 new rhizomes for a percent increase in the new generation of 61.5. Mean length of new rhizomes was 32.6 mm with a range from 10 to 45 mm. The number of rhizome buds with flower primordia was 19 while two had none.

In Treatment 3, with light energy at 1.5 uW/cm^2 and soil temperature controlled by ambient chamber temperature, 15 parent plants survived and produced 24 new rhizomes for a percent increase in the new generation of 60. Mean length of new rhizomes was 28.6 mm with a range from 13 to 54 mm. All 24 new rhizome buds produced flower primordia.

In Treatment 4, with light energy at 1.5 uW/cm^2 and soil temperature always below 16.5^0 C, 14 parent plants survived and produced 23 new rhizomes for a percent increase in the new generation of 64.3. Mean length of new rhizomes was 35.9 mm with a range from 20 to 65 mm. The number of rhizome buds with flower primordia was 22 while one had none.

Table 8 presents the percent TNC content of the underground portions of Clintonia borealis for specimens maintained under the growth chamber conditions.

In Treatment 1, the percent TNC content for old rhizomes was 37.8, for new rhizomes 36.7, and for the roots of new rhizomes 31.2.
In Treatment 2, the percent TNC content for old rhizomes was 36.4, for new rhizomes 30.8, and for the roots of new rhizomes 38.4.
In Treatment 3, the percent TNC content for old rhizomes was 37.1, for new rhizomes 38.8, and for the roots of new rhizomes 42.3.
In Treatment 4, the percent TNC content for old rhizomes was 36.5, for new rhizomes 32.1 and for the roots of new rhizomes 37.6.

TABLE 7

SUMMARY OF RESULTS ON RHIZOME AND INFLORESCENCE PRIMORDIA PRODUCTION FOR *Clintonia borealis* MAINTAINED UNDER CONDITIONS OF VARIED SOIL TEMPERATURES AND LIGHT ENERGY LEVELS

	Treatment 1	Treatment 2	Treatment 3	Treatment 4
# of Parent Plants Surviving	13	13	15	14
# of New Rhizomes Produced	22	21	24	23
Percent Increase for New Generation	69.2%	61.5%	60%	64.3%
Mean Length of New Rhizomes	33 mm	32.6 mm	28.6 mm	35.9 mm
Range of Lengths of New Rhizomes	11-50 mm	10-45 mm	13-54 mm	20-65 mm
# of Buds with Flower Primordia	21	19	24	22
# of Buds Without Flower Primordia	1	2	0	1

TABLE 8

PERCENT TNC CONTENT (DRY WEIGHT BASIS) OF THE UNDERGROUND PORTIONS OF *Clintonia borealis* MAINTAINED UNDER CONDITIONS OF VARIED SOIL TEMPERATURES AND LIGHT ENERGY LEVELS

	Treatment 1	Treatment 2	Treatment 3	Treatment 4
Percent TNC Content of Old Rhizomes	37.8%	36.4%	37.1%	36.5%
Percent TNC Content of New Rhizomes	36.7%	30.8%	38.8%	32.1%
Percent TNC Content of Roots of New Rhizomes	31.2%	38.4%	42.3%	37.6%
Average Percent TNC Content For All Systems	35.2%	35.2%	39.4%	35.4%

DISCUSSION

All factors considered, survival and growth of specimens of Clintonia borealis under controlled conditions was felt to be very good.

Practically 100 percent survival was attained, with production of new rhizomes being far greater than what was encountered with specimens collected from the field during the fall of 1978 (see section on Primordia). For 3-leaved nonflowering specimens collected during fall 1978 the relative increase in new plants through rhizome production was 25% whereas under chamber conditions all treatments were 60% or better.

Mean length of rhizomes, however, was considered less than typical for the species; 8.29 cm, Utech (1973); and may have resulted from earlier rhizome bud formation in chamber-grown plants than for plants growing in the field. Earlier bud formation could, in part, explain the high frequency of flowering among chamber-grown plants. Practically every plant grown produced rhizomes containing an obvious primordial inflorescence. The difference as compared to plants collected from the field is quite dramatic, when one considers that 3-leaved nonflowering specimens collected during the fall 1978 had a flowering success ratio of only 0.20 (mature apices). It is suggested that energy normally channelled into rhizome elongation was instead used for flower formation.

Total nonstructural carbohydrate content in old and new rhizomes compares favourably to the levels found in field-collected specimens at the end of the 1978 growing season (see section on Nonstructural Carbohydrates). In all treatments, levels were between 30 and 40 percent. The inclusion of roots of newly produced rhizomes in the analysis demonstrated that these structures were also capable of storing a considerable amount of TNC and thus provide an important secondary energy reserve.

The anticipated differences between treatments with respect to the amount of stored TNC and the production of a primordial inflorescence by new rhizomes were not realized. It was hoped that the soil temperature and light level conditions provided would result in low TNC reserves and no flowering amongst certain treatments. The fact that plants were so successful in producing flowers and storing carbohydrate can perhaps be attributed to the artificially long days in the chamber (16 hours) which could offset low light energy levels.

A soil temperature adjacent to the rhizome of less than 16.5° C resulted in new rhizomes with less stored TNC than comparable treatments in which soil temperature fluctuated with ambient chamber temperature. Anderson and Louck (1973) have reported that, for the boreal herb Trientalis borealis Raf., cool night time temperatures (11.9-15.8° C) result in rhizome tubers with greater storage biomass than plants grown under warm night temperatures (20.0°-22° C).

The cooler temperatures are felt to provide a more favourable balance between respiration and photosynthesis. The authors suggest that warm summer temperatures throughout the day in the southern range limits of _T. borealis_ result in higher respiratory rates that deplete carbohydrate reserves and restrict both species' abundance and suitable habitats.

Similar factors may be responsible for limiting the southern distribution of _Clintonia borealis_; however this could not be demonstrated under the chamber conditions provided. Average percent TNC content for all systems was virtually identical in all treatments with the exception of Treatment 3, indicating that either soil temperature differences between treatments were not extreme enough or that air temperature (i.e., leaf temperature) is a more critical factor than soil temperature in governing the level of TNC in underground storage organs.

POPULATION DYNAMICS
AND
DEVELOPMENTAL STUDIES

During 1978, while examining a fall collection of perennating buds for flower primordia, it was found that the buds apparently enter winter at different levels of maturity. That is, leaves and inflorescence primordia within the buds of some plants were of a significantly smaller size and reduced level of differentiation than those found in the buds of other specimens.

Two possible explanations were formulated to explain the observed phenomenon: first, primordial leaves and inflorescences, of reduced size and level of differentiation, would continue their development in the spring, when environmental conditions became more favourable for growth; and second, primordial leaves and inflorescences had to reach a certain level of maturity, prior to the onset of fall dormancy, and failing this, would abort since no further development could take place during the spring.

From the outset the second hypothesis seemed most plausible. When leaf number and the number of flowering individuals in the bud was compared with the parent generation, a marked increase in the number of flowering specimens and a virtual absence of two-leaved plants among the developing generation became obvious. Such a radical shift in the demography of a population seemed very unlikely, barring some major disturbance, of which none was recently apparent.

METHODS

Plants used in this study were collected from George Burke Park, located approximately 1 km north of Lakehead University. The collection dates were November 1, 1978 and the months of May and June, 1979. The study site measured approximately 100 square meters and was dominated by an overstory of mature Populus tremuloides.

The first collection was made two weeks prior to the first winter's snow and consisted of 135 perennating buds along with the 112 parent plants which had produced them. Obviously, the harvested plants, once dissected, could not be replanted to see if either abortion or continued development of flowers and leaves would have occurred so the only alternative was to monitor the development of specimens during the spring when regular collections could be made as the plants expanded.

The spring collections were divided into two groups based on the sampling techniques employed, which was modified once leaf expansion had begun. The sampling dates May 1 and May 8 corresponded to the pre-expansion period and therefore could have included more flowering specimens than the samples taken on May 17, 24 and June 4. These latter sample dates spanned the period from first expansion to complete expansion of leaves and elongation of flower-bearing stipes and thus obvious flowering specimens were not included. Furthermore, no data were obtained on the condition of the parent plants, with regard to leaf number and presence of a flower-bearing stipe, since these plants had deteriorated too much, by this time, to be of use.

Plants were harvested with a trowel and the whole plant along with its rhizome was returned to the laboratory for examination. Examination consisted of noting the number of leaves and evidence of flowering (presence of at least part of the dried flower-bearing stipe on the parent plant), and the number of new rhizomes produced. In addition, each rhizome bud was dissected with fine forceps and examined for developing leaves and flowers using a dissecting microscope with a magnification of up to 25X. Freehand drawings of representative examples of the developing apices were made following staining in a .05% solution of acid Fuchsin in 95% ETOH for 48 hours.

To describe the observed differences in appearance between apices, a system of classification was constructed for both leaves and flowers, which divided the various types into groups based on their level of differentiation and relative size. For flower primordia, the following categories were created: mature; partially mature; and immature. Mature flower primordia had an inflorescence with all flower parts (tepals, anthers and pistil) differentiated plus a well developed stipe. Partially mature primordia had an inflorescence with some to all flower parts differentiated but the stipe was short. An immature flower primordium had an incompletely differentiated inflorescence that remained in close association with the meristem.

Well developed leaves formed part of a tight whorl of at least two leaves and were thus classed as preformed, while all others not associated with this whorl (smaller, less differentiated leaves) were classed as primordial.

A final category, called potentials, designated apices in which it could not be stated with certainty, due to their minuteness, that a developing inflorescence or leaf was being produced prior to harvesting. In instances of this sort, an apex would be classed as both a potential inflorescence and a potential leaf.

RESULTS

Figures 1 through 7 illustrate diagramatically the various categories of apices present in spring and fall bud collections. Distinct levels of maturity are readily apparent among developing inflorescences.

Table 9 is a summary of the data on the numbers of flowering and nonflowering plants of Clintonia borealis collected during the fall of 1978 together with the estimated percent contribution of each type toward the total population. Three-leaved nonflowering plants were most common among the population, having a percent contribution of 39.3, followed by 2-leaved nonflowering plants (35.7), then 3-leaved flowering plants (13.4), 2-leaved and 4-leaved flowering plants (5.4) and finally 4-leaved nonflowering plants (0.9). On the whole, 3-leaved plants formed the largest group (52.7) then 2-leaved plants (41.1) and lastly 4-leaved plants (6.3). Nonflowering plants outnumbered flowering plants with a percent contribution of 75.9 compared to 24.1.

Table 10 summarizes the data on the number of new rhizome buds produced by the parent generation and the estimated percent contribution by each category of parent plant towards the makeup of the entire population. Three-leaved nonflowering plants had the largest percent contribution of new rhizomes at 40.7 followed by 2-leaved nonflowering plants (31.9), 3-leaved flowering plants (14.8), 4-leaved flowering plants (6.7), 2-leaved flowering plants (5.2) and finally

4-leaved nonflowering plants (0.7). In terms of percent contribution toward the entire population, based on leaf number alone, 3-leaved plants contributed the most (55.6) followed by 2-leaved plants (37.0) and 4-leaved plants (7.4). Nonflowering plants made the largest percent contribution toward new rhizome production (73.3) with flowering plants contributing the remainder (26.7).

Table 11 summarizes the data on the increase in the number of new specimens of Clintonia borealis over the number in the parent generation. The numerical increase was obtained by subtracting the number of parent plants in each group from the number of new rhizomes in each group. Relative percent increase in new plants is the numerical increase in a group as a percentage of the number of specimens of that group within the parent generation. Absolute percent increase in new plants is the numerical increase in plants in a group as a percentage of the total number of parent plants collected (i.e., 112).

In terms of relative percent increase in new plants, when the number of leaves on the parent plant and presence or absence of flowers were considered together, 4-leaved nonflowering plants demonstrated the largest percent increase at 50.0 followed by 3-leaved flowering plants (33.3), 3-leaved nonflowering plants (25.0), 2-leaved flowering plants (16.7), 2-leaved nonflowering plants (7.5) and 4-leaved flowering plants (0). As a function of leaf number only, 4-leaved plants had the highest percent increase (42.9) followed by 3-leaved plants (27.1) and 2-leaved plants (8.7). Flowering and nonflowering plants demonstrated almost identical relative percent increases of 22.2 and 20.0 respectively.

In relation to absolute percent increase in new plants, when the number of leaves on the parent plant and presence or absence of flowers were considered, 3-leaved nonflowering specimens were first at 9.8 followed by 3-leaved flowering plants (4.5), 4-leaved and 2-leaved nonflowering plants (2.7), 2-leaved flowering (0.9) and 4-leaved flowering (0). As a function of leaf number alone, 3-leaved plants showed the largest percent increase at 14.3 followed by 2-leaved plants (3.6) and finally 4-leaved plants (2.7). Nonflowering plants demonstrated the largest contribution to the absolute percent increase at 15.2 while the contribution by flowering plants was 5.4.

Table 12 details the results of the examination of rhizome bud apices of <u>Clintonia borealis</u> for developing inflorescences. The bracketed figures indicate the number of apices for each class; either potential flowering, immature, partially mature or fully mature, followed by the total for each type of parent plant. Results for 2-leaved nonflowering parents were (13), (4), (1), (0) = 18 and for 2-leaved flowering parents (0), (0), (0), (2) = 2. For 3-leaved nonflowering plants the figures were (12), (7), (4), (11) = 34 and for 3-leaved flowering parents (9), (1), (1), (7) = 18. For 4-leaved nonflowering parents the figures were (0), (0), (0), (0) = 0 and for 4-leaved flowering parents (1), (0), (1), (5) = 7. Total for all potential flowering apices were 35, immature 12, partially mature 7 and fully mature 25. Total for all of the above classes of apices was 79.

Table 13 presents the theoretical number of flowering plants of Clintonia borealis that could arise in 1979 from the rhizome buds of the parent generation, assuming only certain classes of developing apices are successful. Assuming complete development of all but potential flowering apices, 5 flowering plants would be produced from forty 2-leaved nonflowering parents, 2 from six 2-leaved flowering parents, 22 from forty-four 3-leaved nonflowering parents, 9 from fifteen 3-leaved flowering parents, 0 from one 4-leaved nonflowering parent, and 6 from six 4-leaved flowering parents for a total of 44 flowering plants in the 1979 generation.

Assuming complete development of all but potential and immature flowering apices, 1 flowering plant would be produced from forty 2-leaved nonflowering parents, 2 from six 2-leaved flowering parents, 15 from forty-four 3-leaved nonflowering parents, 8 from fifteen 3-leaved flowering parents, 0 from one 4-leaved nonflowering parent and 6 from six 4-leaved flowering parents for a total of 32 flowering plants in the 1979 generation.

Assuming the mature apices only complete their development, 0 flowering plants would be produced from forty 2-leaved nonflowering parents, 2 from six 2-leaved flowering parents, 11 from forty-four

3-leaved nonflowering parents, 7 from fifteen 3-leaved flowering parents, 0 from one 4-leaved nonflowering parent and 5 from six 4-leaved flowering parents for a total of 25 flowering plants in the 1979 generation.

Table 14 presents the success ratio for flowering in the study population of Clintonia borealis. The success ratio was calculated by dividing the number of flowering apices in each group (from Table 13) by the number of rhizomes produced by the corresponding category of parent plant (from Table 10). The success ratio is therefore a measure of the likelihood that a particular category of parent plant will produce a flowering offspring.

Assuming all but potential flowering apices complete their development, the success ratio for 2-leaved nonflowering parents was 0.10, for 2-leaved flowering parents 0.04, 3-leaved nonflowering parents 0.29, 3-leaved flowering parents 0.12, 4-leaved nonflowering parents 0, and 4-leaved flowering parents 0.60 for an average success ratio of 0.33.

Assuming all but potential and immature flowering apices complete their development, the success ratio for 2-leaved nonflowering parents was 0.02, for 2-leaved flowering parents 0.04, 3-leaved nonflowering parents 0.20, 3-leaved flowering parents 0.11, 4-leaved nonflowering parents 0 and 4-leaved flowering parents 0.60 for an average success ratio of 0.22.

Assuming mature apices only complete their development, the success ratio for 2-leaved nonflowering parents was 0, for 2-leaved flowering parents 0.04, 3-leaved nonflowering parents 0.15, 3-leaved flowering parents 0.09, 4-leaved nonflowering parents 0 and 4-leaved flowering parents 0.50 for an average success ratio of 0.19.

Table 15 summarizes the results for the total number and percentage of rhizome buds of Clintonia borealis without flower primordia. If potential flowering apices are excluded, then 25 nonflowering plants would be produced from forty 2-leaved nonflowering parents, 5 from six 2-leaved flowering parents, 21 from forty-four 3-leaved nonflowering parents, 2 from fifteen 3-leaved flowering parents, 1 from one 4-leaved nonflowering parent, and 2 from six 4-leaved flowering parents for a total of 56 nonflowering plants developing in the 1979 generation.

If potential flowering apices are included in the count of nonflowering apices, then 38 nonflowering plants would be produced from forty 2-leaved nonflowering parents, 5 from six 2-leaved flowering parents, 33 from forty-four 3-leaved nonflowering parents, 11 from fifteen 3-leaved flowering parents, 1 from one 4-leaved nonflowering parent and 3 from six 4-leaved flowering parents for a total of 91 nonflowering plants developing in the 1979 generation.

The percentage of the population comprised of nonflowering specimens would then be 41.5 if potential flowering apices are excluded and 67.4 if they are included compared to 75.9 for the percentage of nonflowering specimens in the parent generation.

Table 16 presents the results for the examination of the rhizome buds of Clintonia borealis for developing leaves. The condition of the parent plant with respect to leaf number and presence or absence of flowers is indicated opposite the totals for leaf number in the developing rhizome bud. It was presumed that little, if any, further leaf development in the rhizome buds would have occurred had the plants been left unharvested, since dormancy was imminent.

Dissection revealed the following among the rhizomes of 2-leaved nonflowering parents: 1 with 2 preformed leaves, 3 with 2 preformed leaves plus 1 potential leaf, 18 with 2 preformed leaves plus 1 primordial leaf, 2 with 2 preformed leaves plus 1 primordial and 1 potential leaf, 9 with 3 preformed leaves, 8 with 3 preformed plus 1 potential leaf, 2 with 3 preformed plus 1 primordial leaf, 0 with 3 preformed plus 1 primordial and 1 potential leaf, and 0 with 4 or greater.

Among the rhizomes of 2-leaved flowering parents, 0 had 2 preformed leaves, 0 had 2 preformed leaves plus 1 potential leaf, 5 had 2 preformed leaves plus 1 primordial leaf, 0 had 2 preformed leaves plus 1 primordial and 1 potential leaf, 1 had 3 preformed leaves, 0 had any greater than 3 but less than 4, 1 had 4 preformed leaves, and 0 had any greater than 4.

Among the rhizomes of 3-leaved nonflowering parents, 0 had 2 preformed leaves, 0 had 2 preformed leaves plus 1 potential leaf, 12 had 2 preformed leaves plus 1 primordial leaf, 0 had 2 preformed leaves plus 1 primordial and 1 potential leaf, 24 had 3 preformed leaves, 12 had 3 preformed leaves plus 1 potential leaf, 4 had 3 preformed leaves plus 1 primordial leaf, 0 had 3 preformed leaves plus 1 primordial and 1 potential leaf, 3 had 4 preformed leaves, and 0 had any greater than 4.

Among the rhizomes of 3-leaved flowering plants, 1 had 2 preformed leaves, 1 had 2 preformed leaves plus 1 potential leaf, 1 had 2 preformed leaves plus 1 primordial leaf, 1 had 2 preformed leaves plus 1 primordial and 1 potential leaf, 6 had 3 preformed leaves, 7 had 3 preformed leaves plus 1 potential leaf, 0 had 3 preformed leaves plus 1 primordial leaf, 0 had 3 preformed leaves plus 1 primordial and 1 potential leaf, 3 had 4 preformed leaves and 0 had any greater than 4.

Among the rhizomes of 4-leaved nonflowering parents, the single example collected had 3 preformed leaves while among those from 4-leaved flowering parents 1 had 2 preformed leaves, 0 had greater than 2 but less than 3, 4 had 3 preformed leaves, 1 had 3 preformed leaves plus 1 potential leaf, 1 had 3 preformed leaves plus 1 primordial leaf, 0 had 3 preformed leaves plus 1 primordial and 1 potential leaf, 2 had 4 preformed leaves, and 0 had any greater than 4.

Total number of rhizomes in each category was 3 with 2 preformed leaves, 4 with 2 preformed leaves plus 1 potential leaf, 36 with 2 preformed leaves plus 1 primordial leaf, 3 with 2 preformed leaves plus 1 primordial and 1 potential leaf, 45 with 3 preformed leaves, 28 with 3 preformed leaves plus 1 potential leaf, 7 with 3 preformed leaves plus 1 primordial leaf, 0 with 3 preformed leaves plus 1 primordial and 1 potential leaf, 9 with 4 preformed leaves, and 0 with any greater than 4.

Table 17 presents the theoretical numbers of leaves of Clintonia borealis that could arise in 1979 from the rhizome buds of the parent generation, assuming either (1) preformed and primordial leaves only complete their development or (2) preformed leaves only complete their development. The totals for each column represent the makeup of the new generation (1979) with respect to the number of plants in each leaf-number class.

If the first hypothesis is presumed true, then the new generation would consist of seven 2-leaved plants, one hundred and twelve 3-leaved plants and sixteen 4-leaved plants, whereas if the second hypothesis is correct, then the new generation would consist of forty-six 2-leaved plants, eighty 3-leaved plants and nine 4-leaved plants.

Table 18 presents the percentage distribution of leaves for the study population of Clintonia borealis comparing the parent generation to two possible offspring generations created on the premise that only certain leaves within the rhizome bud will successfully complete their development.

Within the parent generation 41.1% of the plants had two leaves, 52.7% had three leaves and 6.3% had four leaves. Assuming preformed and primordial leaves only complete their development in the new generation, 5.2% would have two leaves, 83.0% would have three leaves and 11.9% would have four leaves. Assuming preformed leaves only complete their development, 34.1% would have two leaves, 59.3% would have three leaves and 6.7% would have four leaves.

Table 19 presents the results of the examination of the spring collection of pre-expansion rhizome buds of Clintonia borealis for developing inflorescences. For the collection dates May 1 and May 8, 1979 the figures for the number of potential flower primordia were 5 and 17 respectively, for immature flower primordia 3 and 1 respectively, partially mature flower primordia 2 and zero respectively and mature flower primordia 2 and 1 respectively. The number of buds without flower primordia, excluding potentials, was 11 and 14 respectively and including potentials 16 and 31 respectively. The number of buds examined on May 1 was 23 and on May 8 was 33.

Table 20 presents the results of the examination of the spring collection of post-expansion rhizome buds of Clintonia borealis for developing inflorescences. For the collection dates May 17, May 24, and June 4, 1979 the number of potential flower primordia was 15, 11 and 14 respectively, for immature flower primordia 2, 4 and 5 respectively, partially mature flower primordia zero, 1 and zero respectively, and mature flower primordia zero, 1 and zero respectively. The number of buds without flower primordia, excluding potentials, was 12, 9 and 6 respectively and, including potentials, 27, 20 and 20. The number of buds examined on May 17 was 29, on May 24 was 26 and on June 4 was 25.

Table 21 outlines the results of the examination of a spring collection of pre-expansion rhizome buds of Clintonia borealis for developing leaves. For the collection dates May 1 and May 8, 1979 the number of buds with 2 preformed leaves was 2 and zero respectively; with 2 preformed plus 1 potential leaf, 1 and 3 respectively; with 2 preformed plus 1 primordial leaf, 5 and 12 respectively; with 2 preformed plus 1 primordial and 1 potential leaf, zero and 3 respectively; with 3 preformed leaves, 8 and 4 respectively; with 3 preformed plus 1 potential leaf, 6 and 9 respectively; with 3 preformed plus 1 primordial leaf, 1 and zero respectively; with 3 preformed plus 1 primordial and 1 potential leaf, zero and 1 respectively; and none with 4 or more leaves, with the exception of 1 bud with 4 preformed plus 1 potential leaf in the May 8 collection. Total number of buds examined was 23 for May 1 and 33 for May 8.

Table 22 outlines the results of the examination of a spring collection of post-expansion rhizome buds of Clintonia borealis for developing leaves. For the collection dates May 17, 24 and June 4, 1979 the number of buds with 2 preformed leaves was zero, 1 and zero respectively; with 2 preformed plus 1 potential leaf, 3, 1 and 1 respectively; with 2 preformed plus 1 primordial leaf, 12, 4 and 4 respectively;

with 2 preformed plus 1 primordial and 1 potential leaf, 3, 1 and 1 respectively; with 3 preformed leaves, 2, 3 and 5 respectively; with 3 preformed plus 1 potential leaf, 7, 8 and 10 respectively; with 3 preformed plus 1 primordial leaf, zero, 4 and 3 respectively; with 3 preformed plus 1 primordial and 1 potential leaf, 2, zero and 1 respectively; and none with 4 or more with the exception of 3 buds with 4 preformed leaves and 1 bud with 4 preformed plus 1 primordial leaf, both collected on May 24. The total number of buds examined on May 17 was 29, on May 24 was 26 and on June 4 was 25.

Figure 1. An inflorescence dissected from the rhizome bud of *Clintonia borealis*. This inflorescence was classed as "fully mature" since all flower parts were formed and the stipe was long. Collection date: Nov. 1, 1978. Magnification 13X.

(1) flower (2) stipe

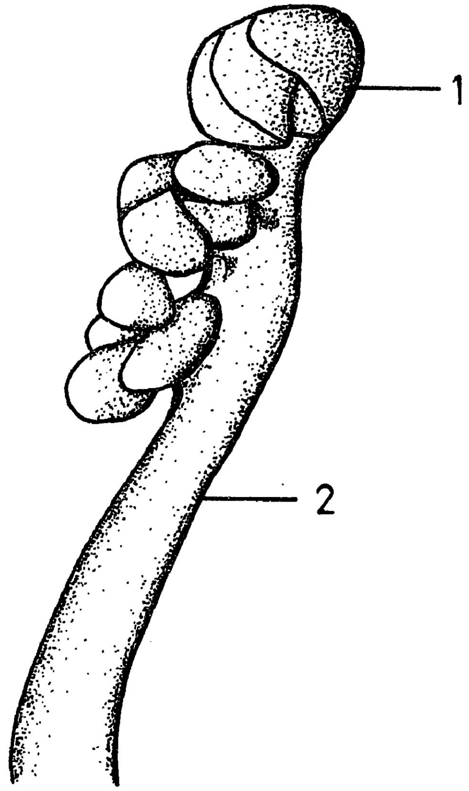

1
2

Figure 2. An inflorescence dissected from the rhizome bud of *Clintonia borealis*. This inflorescence, collected May 1, 1979, was classed as "fully mature" and was felt to be at the same stage of development as fully mature inflorescences collected on November 1, 1978 (see Figure 1). Magnification 13X.

(1) flower (2) stipe

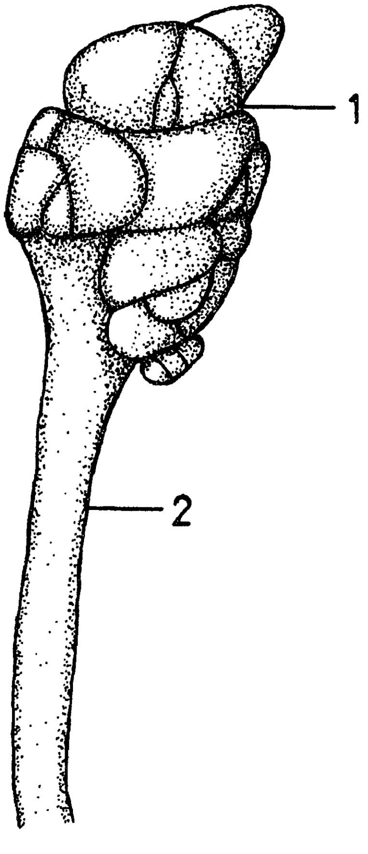

1
2

Figure 3. An inflorescence dissected from the developing rhizome bud of *Clintonia borealis*. The short stipe and partially formed flowers placed this specimen in the group labelled "partially mature" inflorescences. Collection date: Nov. 1, 1978. Magnification 50X.

(1) developing flower (2) stipe

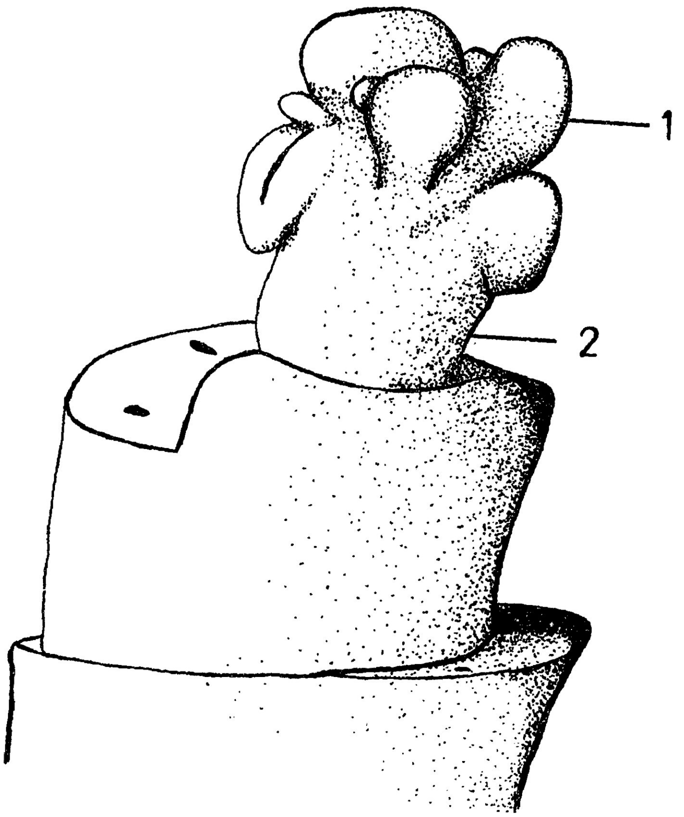

1
2

Figure 4. An inflorescence dissected from the rhizome bud of Clintonia borealis. Such an inflorescence was classed as "immature" on the basis of its apparent retarded development of flowers and stipe.
Collection date: Nov. 1, 1978. Magnification 38X.

(1) developing flower

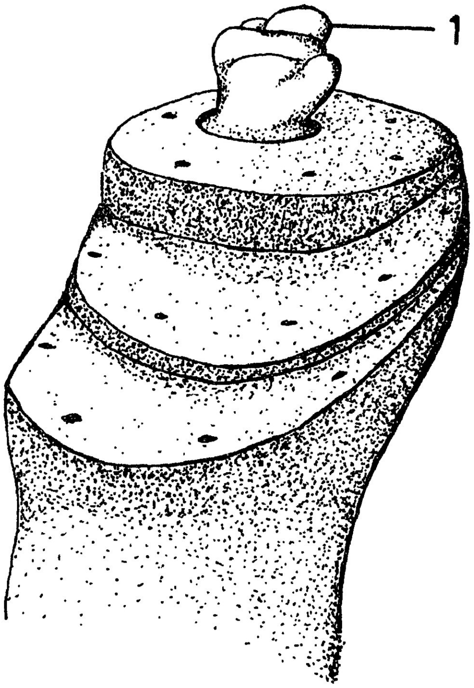

1

Figure 5. An inflorescence dissected from the rhizome bud of *Clintonia borealis*. An example of an "immature" inflorescence (see Figure 4), collected on May 8, 1979, that was considered to be at the same level of development as immature types collected on Nov. 1, 1978. Magnification 40X.

(1) developing flower

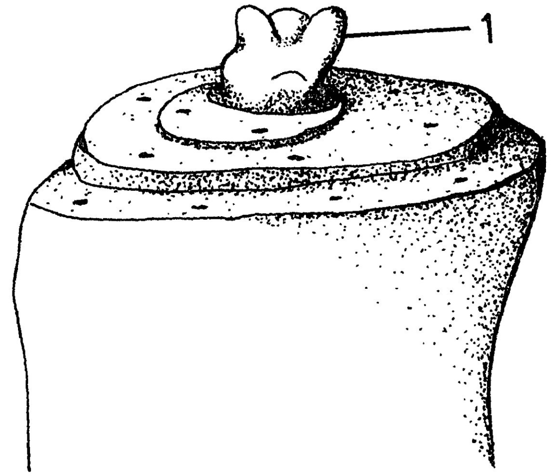

1

Figure 6. A developing leaf dissected from the rhizome bud of Clintonia borealis. A leaf of this type was classed as "primordial" on the basis of size relative to that of other leaves within the bud. Other leaves averaged approximately 2 cm in length and formed part of a tight whorl ensheathing the primordial leaf. Primordial leaves were present in the Nov. 1, 1978 collection and also the May and June 1979 collections. Magnification 35X.

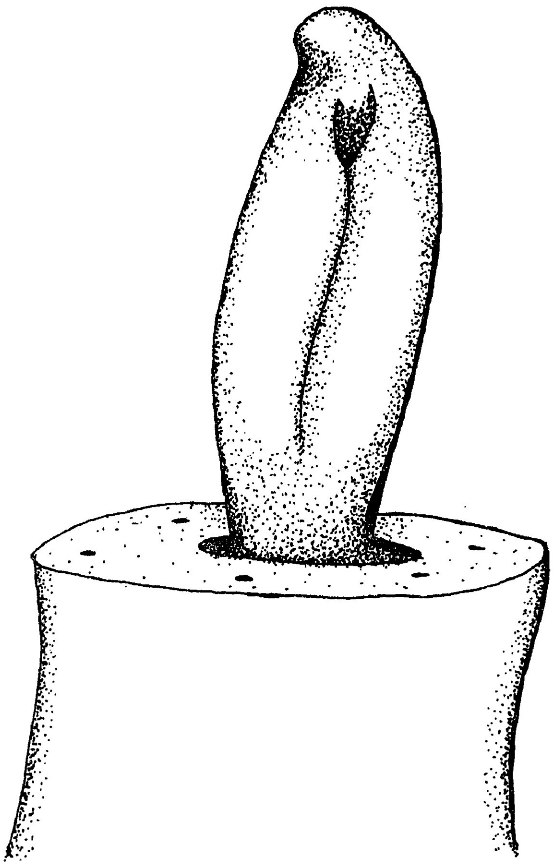
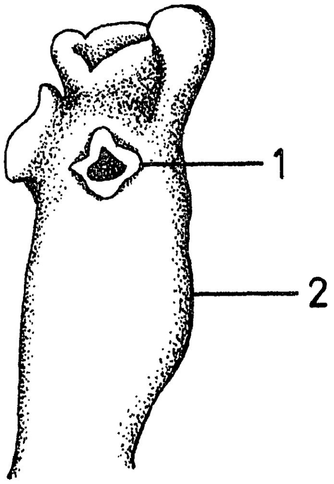


Figure 7. Aborted inflorescences dissected from the rhizome bud of *Clintonia borealis*. The stipes are short and the developing flowers shrivelled. Collection date: June 4, 1979. Magnification 52X.

(1) shrivelled flower (2) stipe


1
2

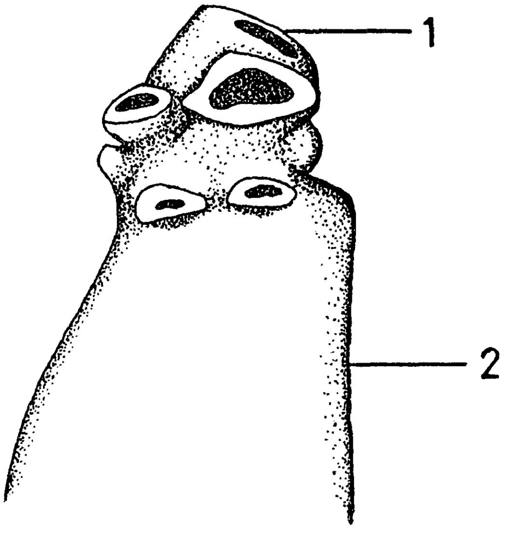

1
2

TABLE 9

SUMMARY OF DATA ON NUMBERS OF PARENT PLANTS AND PERCENT CONTRIBUTION OF EACH TYPE FOR SPECIMENS OF *Clintonia borealis* COLLECTED ON NOVEMBER 1, 1978

# of Flowering Plants Collected	% Contribution
2-leaved - 6	5.4
3-leaved - 15	13.4
4-leaved - 6	5.4
Total - 27	24.2

# of Nonflowering Plants Collected	% Contribution
2-leaved - 40	35.7
3-leaved - 44	39.3
4-leaved - 1	0.9
Total - 85	75.9

# of Flowering and Nonflowering Plants Collected	% Contribution
2-leaved - 46	41.1
3-leaved - 59	52.7
4-leaved - 7	6.3
Total - 112	

TABLE 10

SUMMARY OF DATA ON NUMBERS OF RHIZOME BUDS PRODUCED AND THE PERCENT CONTRIBUTION BY PARENT PLANTS BASED ON LEAF NUMBER AND PRESENCE OR ABSENCE OF FLOWERS, FOR SPECIMENS OF *Clintonia borealis* COLLECTED ON NOVEMBER 1, 1978

# of Buds Produced by Flowering Plants	% Contribution
2-leaved - 7	5.2
3-leaved - 20	14.8
4-leaved - 9	6.7
Total - 36	26.7

# of Buds Produced by Nonflowering Plants	% Contribution
2-leaved - 43	31.9
3-leaved - 55	40.7
4-leaved - 1	0.7
Total - 99	73.3

# of Buds Produced by Flowering and Nonflowering Plants	% Contribution
2-leaved - 50	37.0
3-leaved - 75	55.6
4-leaved - 10	7.4
Total - 135	

TABLE 11

TOTAL INCREASE AND RELATIVE AND ABSOLUTE PERCENT INCREASES IN THE NUMBER OF RHIZOMES OVER THE PARENT GENERATION BASED ON LEAF NUMBER AND PRESENCE OR ABSENCE OF FLOWERS, FOR SPECIMENS OF *Clintonia borealis* COLLECTED ON NOVEMBER 1, 1978

# of New Rhizomes Produced Minus # of Parent Plants	Relative % Increase Over Parent Generation	Absolute % Increase Over Parent Generation
2-leaved nonflowering - 3	7.5	2.7
2-leaved flowering - 1	16.7	0.9
3-leaved nonflowering - 11	25.0	9.8
3-leaved flowering - 5	33.3	4.5
4-leaved nonflowering - 0	0	0
4-leaved flowering - 3	50.0	2.7
2-leaved plants - 4	8.7	3.6
3-leaved plants - 16	27.1	14.3
4-leaved plants - 3	42.9	2.7
nonflowering plants - 14	16.5	12.5
flowering plants - 9	33.3	8.0

TABLE 12

RESULTS OF THE EXAMINATION OF RHIZOME BUD APICES, OF *Clintonia borealis*, FOR DEVELOPING INFLORESCENCES.

The categories that were created to describe the observed differences between apices are listed across the top, while the column on the left indicates the condition of the parent plant.

Parent Plant	Potential	Immature	Partially Mature	Fully Mature	Total
2-leaved nonflowering	13	4	1	0	18
2-leaved flowering	0	0	0	2	2
3-leaved nonflowering	12	7	4	11	34
3-leaved flowering	9	1	1	7	18
4-leaved nonflowering	0	0	0	0	0
4-leaved flowering	1	0	1	5	7
TOTAL	35	12	7	25	79

TABLE 13

THEORETICAL NUMBERS OF FLOWERING PLANTS OF *Clintonia borealis* THAT COULD ARISE IN 1979 FROM THE RHIZOME BUDS OF THE PARENT GENERATION

A IF ALL BUT POTENTIAL FLOWERING APICES COMPLETE THEIR DEVELOPMENT.

Parent Plant	Total	# of Specimens in Parent Generation
2-leaved nonflowering	5	40
2-leaved flowering	2	6
3-leaved nonflowering	22	44
3-leaved flowering	9	15
4-leaved nonflowering	0	1
4-leaved flowering	6	6
	44	

B IF ALL BUT POTENTIAL AND IMMATURE FLOWERING APICES COMPLETE THEIR DEVELOPMENT.

Parent Plant	Total	# of Specimens in Parent Generation
2-leaved nonflowering	1	40
2-leaved flowering	2	6
3-leaved nonflowering	15	44
3-leaved flowering	8	15
4-leaved nonflowering	0	1
4-leaved flowering	6	6
	32	

C IF MATURE APICES ONLY COMPLETE THEIR DEVELOPMENT.

Parent Plant	Total	# of Specimens in Parent Generation
2-leaved nonflowering	0	40
2-leaved flowering	2	6
3-leaved nonflowering	11	44
3-leaved flowering	7	15
4-leaved nonflowering	0	1
4-leaved flowering	5	6
	25	

TABLE 14

SUCCESS RATIO FOR FLOWERING IN A POPULATION OF *Clintonia borealis*

A IF ALL BUT POTENTIAL FLOWERING APICES COMPLETE THEIR DEVELOPMENT.

Parent Plant	Success Ratio
2-leaved nonflowering	0.12
2-leaved flowering	0.29
3-leaved nonflowering	0.40
3-leaved flowering	0.45
4-leaved nonflowering	0
4-leaved flowering	0.67
AVERAGE	0.32

B IF ALL BUT POTENTIAL AND IMMATURE FLOWERING APICES COMPLETE THEIR DEVELOPMENT.

Parent Plant	Success Ratio
2-leaved nonflowering	0.02
2-leaved flowering	0.29
3-leaved nonflowering	0.27
3-leaved flowering	0.40
4-leaved nonflowering	0
4-leaved flowering	0.67
AVERAGE	0.28

C IF MATURE APICES ONLY COMPLETE THEIR DEVELOPMENT.

Parent Plant	Success Ratio
2-leaved nonflowering	0
2-leaved flowering	0.29
3-leaved nonflowering	0.20
3-leaved flowering	0.35
4-leaved nonflowering	0
4-leaved flowering	0.55
AVERAGE	0.23

TABLE 15

TOTAL NUMBER AND PERCENTAGE OF RHIZOME BUDS OF *Clintonia borealis* WITHOUT INFLORESCENCE PRIMORDIA

A EXCLUDING POTENTIAL FLOWERING APICES.

Parent Plant	Total	Parent Generation
2-leaved nonflowering	25	40
2-leaved flowering	5	6
3-leaved nonflowering	21	44
3-leaved flowering	2	15
4-leaved nonflowering	1	1
4-leaved flowering	2	6
	56	

B INCLUDING POTENTIAL FLOWERING APICES.

Parent Plant	Total	Parent Generation
2-leaved nonflowering	38	40
2-leaved flowering	5	6
3-leaved nonflowering	33	44
3-leaved flowering	11	15
4-leaved nonflowering	1	1
4-leaved flowering	3	6
	91	

PERCENTAGE OF POPULATION NONFLOWERING

A	41.5
B	67.4
Parent Generation	75.9

TABLE 16

RESULTS OF THE EXAMINATION OF THE RHIZOME BUDS OF *Clintonia borealis* FOR DEVELOPING LEAVES. SPECIMENS COLLECTED ON NOVEMBER 1, 1978

THE HEADING AT THE TOP OF EACH COLUMN INDICATES THE NUMBER OF DEVELOPING LEAVES WITHIN THE BUD. FOR EXAMPLE, 3+* COVERS BUDS WITH 3 PREFORMED LEAVES PLUS 1 PRIMORDIAL LEAF AND 1 POTENTIAL LEAF.

Parent Plant	2	2*	2+	2+*	3	3*	3+	3+*	4	4*	4+	4+*
2-leaved nonflowering	1	3	18	2	9	8	2	0	0	0	0	0
2-leaved flowering	0	0	5	0	1	0	0	0	1	0	0	0
3-leaved nonflowering	0	0	12	0	24	12	4	0	3	0	0	0
3-leaved flowering	1	1	1	1	6	7	0	0	3	0	0	0
4-leaved nonflowering	0	0	0	0	1	0	0	0	0	0	0	0
4-leaved flowering	1	0	0	0	4	1	1	0	2	0	0	0
TOTAL	3	4	36	3	45	28	7	0	9	0	0	0

\+ Indicates Primordial Leaf
* Indicates Potential Leaf

TABLE 17

THEORETICAL NUMBERS OF LEAVES OF *Clintonia borealis* THAT COULD ARISE IN 1979 FROM THE RHIZOME BUDS OF THE PARENT GENERATION

A IF PREFORMED AND PRIMORDIAL LEAVES ONLY COMPLETE THEIR DEVELOPMENT.

Parent Plant	2	3	4
2-leaved nonflowering	4	37	2
2-leaved flowering	0	6	1
3-leaved nonflowering	0	48	7
3-leaved flowering	2	15	3
4-leaved nonflowering	0	1	0
4-leaved flowering	1	5	3
TOTAL	7	112	16

B IF PREFORMED LEAVES ONLY COMPLETE THEIR DEVELOPMENT.

Parent Plant	2	3	4
2-leaved nonflowering	24	19	0
2-leaved flowering	5	1	1
3-leaved nonflowering	12	40	3
3-leaved flowering	4	13	3
4-leaved nonflowering	0	1	0
4-leaved flowering	1	6	2
TOTAL	46	80	9

TABLE 18

PERCENT DISTRIBUTION OF LEAVES FOR A POPULATION OF *Clintonia borealis*

PARENT GENERATION

2-leaved plants - 41.1%
3-leaved plants - 52.7%
4-leaved plants - 6.3%

A IF PREFORMED AND PRIMORDIAL LEAVES ONLY COMPLETE THEIR DEVELOPMENT.

2-leaved plants - 5.2%
3-leaved plants - 83.0%
4-leaved plants - 11.9%

B IF PREFORMED LEAVES ONLY COMPLETE THEIR DEVELOPMENT.

2-leaved plants - 34.1%
3-leaved plants - 59.3%
4-leaved plants - 6.7%

TABLE 19

EXAMINATION OF A SPRING COLLECTION OF PRE-EXPANSION RHIZOME BUDS OF *Clintonia borealis* FOR DEVELOPING INFLORESCENCES. BUDS COLLECTED DURING 1979.

	May 1 # of Buds	May 8 # of Buds
Number of Potential Flower Primordia	5	17
Number of Immature Flower Primordia	3	1
Number of Partially Mature Flower Primordia	2	0
Number of Mature Flower Primordia	2	
Number of Buds Without Flower Primordia	A-11 B-16	A-14 B-31
Number of Buds Examined	23	33

A excludes potential flower primordia

B includes potential flower primordia

TABLE 20

EXAMINATION OF A SPRING COLLECTION OF POST-EXPANSION RHIZOME BUDS OF *Clintonia borealis* FOR DEVELOPING INFLORESCENCES. BUDS COLLECTED DURING 1979.

	May 17	May 24	June 4
	# of Buds	# of Buds	# of Buds
Number of Potential Flower Primordia	15	11	14
Number of Immature Flower Primordia	2	4	5
Number of Partially Mature Flower Primordia	0	1	0
Number of Mature Flower Primordia	0	1	0
Number of Buds Without Flower Primordia	A-12 B-27	A-9 B-20	A-6 B-20
Number of Buds Examined	29	26	25

A excludes potential flower primordia

B includes potential flower primordia

TABLE 21

EXAMINATION OF A SPRING COLLECTION OF PRE-EXPANSION RHIZOME BUDS OF *Clintonia borealis* FOR DEVELOPING LEAVES. BUDS COLLECTED DURING 1979.

Number of Developing Leaves	May 1 # of Buds	May 8 # of Buds
2	2	0
2*	1	3
2+	5	12
2+*	0	3
3	8	4
3*	6	9
3+	1	0
3+*	0	1
4	0	0
4*	0	1
4+	0	0
4+*	0	0
Number of Buds Examined	23	33

\+ Indicates Primordial Leaf

* Indicates Potential Leaf

TABLE 22

EXAMINATION OF A SPRING COLLECTION OF POST-EXPANSION RHIZOME BUDS OF *Clintonia borealis* FOR DEVELOPING LEAVES. BUDS COLLECTED DURING 1979.

Number of Developing Leaves	May 17 # of Buds	May 24 # of Buds	June 4 # of Buds
2	0	1	0
2*	3	1	1
2+	12	4	4
2+*	3	1	1
3	2	3	5
3*	7	8	10
3+	0	4	3
3+*	2	0	1
4	0	3	0
4*	0	1	0
4+	0	0	0
4+*	0	0	0
Number of Buds Examined	29	26	25

+ Indicates Primordial Leaf

* Indicates Potential Leaf

DISCUSSION

From the results several conclusions regarding population makeup and reproductive strategy and behaviour of Clintonia borealis can be made. While the small population studied is felt to be representative of types growing under similar conditions in Northwestern Ontario, the figures may not necessarily be valid for populations in more northerly or southerly latitudes or for populations growing on disturbed or atypical sites.

Three-quarters of the plants making up the population were sterile, indicating that vegetative reproduction is the mainstay of the population. In addition, 3-leaved plants were the most important individuals of the population by virtue of their contribution in numbers towards the total population (52.7%) and by the fact that 13.4% of the population was comprised of 3-leaved fertile individuals, more than double that of 2-leaved and 4-leaved specimens. While 2-leaved plants far exceeded 4-leaved plants in number, 4-leaved plants were the most likely type of all to be fertile. What is interesting is that the reproductive strategy of individual specimens, in terms of energy allocation, became less like that of the population as aboveground biomass increased. That is, the more leaves a particular plant possessed the more likely that plant would be fertile, whereas for the population the greatest proportion of biomass was devoted to the production of strictly vegetative individuals.

A similar trend in the population was seen with regard to an increase in numbers through rhizome production. Taking the population as a whole, nonflowering specimens yielded the largest contribution (12.5%) while 3-leaved plants in general and 3-leaved nonflowering plants in particular made the largest contribution by type (14.3% and 9.8% respectively) indicating once again the importance of 3-leaved types for the population.

In terms of relative percent increase over the parent generation, flowering types were twice as effective as nonflowering types in their ability to produce an increase in population through rhizome production with 4-leaved types being most effective followed by 3-leaved then 2-leaved plants.

From the drawings and data presented on developing inflorescences it is apparent that not all apices were at the same level of developmental maturity at the onset of dormancy. Gunther (1972) had noted the same phenomenon amongst specimens of _C_. _borealis_ grown in the laboratory and had suggested the possibility of abortion of poorly developed inflorescences. Billings _et al._(1965) described abortion of the inflorescences of _Oxyria digyna_ (L.) Hill grown under relatively short photoperiods and related this to a shortage of available carbohydrate, stating that the basic requirements for survival must be met before carbohydrate would be diverted to the production of inflorescences.

By examining the success ratio for inflorescence production of the various types of parent plants, it became clear that plants which had flowered during the previous season were the ones most likely to flower again with the highest success ratio possessed by 4-leaved flowering specimens. This makes sense if flowering plants already occupied the most favourable positions within the understory which, in turn, allowed accumulation of sufficient reserve carbohydrate necessary before floral initiation could begin. Poorest performance was by 2-leaved nonflowering types, which again is understandable if total leaf area and previous flower production are factors affecting inflorescence production in the coming year.

The average success ratio for flowering of 0.23 or 23% (mature apices) is the one that most closely approximated that of the parent population (24.2%). Inclusion of partially mature and immature apices in this average brought the figure up to 32% flowering individuals in the new generation. For plants growing in a stable environment the factors responsible for controlling flower production are likely to remain very constant, and thus the percentage of the population in flower is also likely to remain constant. This lends weight to the argument that abortion of preformed inflorescences of C. borealis does occur and that the likelihood of abortion is inversely related to the level of development reached by primordia at dormancy. One might also speculate about a minimum threshold level of stored carbohydrate that must be present in roots and rhizomes before floral initiation begins. If this level is reached too late in the growing season, the primordia begin their development but fail to reach maturity at dormancy. Whatever the reason, aborted inflorescences were present in the spring 1979 collection and it is this fact most of all that leads the author to speculate that floral abortion is a phenomenon common to _C. borealis_.

Examination of the rhizome buds of _C. borealis_ for developing leaves demonstrated that plants continuously produce leaves up until dormancy but that leaf number of the offspring is likely to be the same as that of the parent plant. Since primordial leaves were found in the spring 1979 collection at a time when plant growth had ceased, the theory that leaf abortion occurs in _C. borealis_ is considered valid. Thus in the new generation leaf number is determined by the number of preformed leaves in the rhizome bud at dormancy. By comparing the percent distribution of leaf number in the new generation with that of the parent generation (Table 18) it is seen that if preformed leaves only complete their development then the new generation closely resembles the parent generation, much more so than if primordial leaves also complete development. Once again, it seems that a stable environment will produce a population very similar to that of the generation before. It is interesting to note that, as with flowering, plants do shift back and forth from one leaf number category to the next, e.g., 2-leaved plants producing 3-leaved offspring and 3-leaved plants producing 2-leaved offspring, just as nonflowering plants can produce flowering plants and vice versa.

As noted in a previous section, Clintonia borealis is apparently a day neutral plant; its flowering behaviour is not affected by photoperiod. Populations growing under identical conditions, with regard to day length, will almost inevitably consist of both flowering and nonflowering individuals.

Disregarding photoperiod as a factor influencing flower production, the author decided to investigate the possibility that the position of a plant within the understory would influence whether or not that plant flowered. In actual fact it would be the conditions experienced by the parent plant during the previous season that determined whether its offspring flowered in the following season, since flowers are preformed in the rhizome bud but remain dormant throughout the winter.

Because light conditions within the understory are not uniform, some plants will receive more light than others. If the quantity and quality of the light is a factor influencing flower production in Clintonia borealis, then this may explain, in part, the flowering behavious of populations in nature. Hall (1955) has noted the dramatic effect of varied light intensity on populations of Cornus canadensis L. growing in nature. With 1% of full sunlight plants barely survived but as sunlight increased to 20% of full, moderate vegetative growth took place while at 50% flowering and fruiting occurred.

FLOWERING OCCURRENCE
IN THE FIELD

It was considered impractical to isolate individual plants in the field and study their flowering behaviour in relation to prevailing light conditions and so a system of sampling was devised to allow comparison of flowering between plants growing in essentially open sites to others in nearby shaded areas.

The site that was selected consisted of a 5 km section of hiking and cross-country ski trails, in Centennial Park, located within the City of Thunder Bay, Ontario. The trail itself varied in width from about 2 to 10 meters and consisted of uphill, downhill and flat sections. The overstory within the park was comprised mainly of *Populus tremuloides* Michx., *Picea mariana* (Mill.) BSP., *Picea glauca* (Moench) Voss and *Betula papyrifera* Marsh., with some clumps of *Thuja occidentalis* L.

Sampling entailed walking the 5 kilometers in 100 pace portions (90 to 100 meters), laying out a one meter quadrat immediately to the right of the trail and one other 10 paces into the understory, then counting the number of fertile and sterile specimens of *Clintonia borealis* within each quadrat. The combined number of quadrats counted totalled 112.

By this method it was hoped that a meaningful comparison of figures for frequency of flowering in an essentially open site to that of an essentially closed site would be achieved. It was felt that any bias inherent in the sampling method would tend to favour flower production in closed sites, since development of the overstory could vary dramatically from one quadrat to the next in the off-trail quadrats.

RESULTS

Table 23 presents the results of the total number of plants in the two sites, number of flowering plants, percent flowering, and frequency and relative frequency of flowering for specimens of *Clintonia borealis* in an open site and a closed site.

For the open site the total number of plants was 634, the number of flowering plants 62, percent flowering 9.8, frequency of flowering 20 and relative frequency of flowering 0.36.

For the closed site the total number of plants was 449, the number of flowering plants 8, percent flowering 1.8, frequency of flowering 7 and relative frequency of flowering 0.13.

TABLE 23

TOTAL NUMBER OF PLANTS, NUMBER OF FLOWERING PLANTS, PERCENT FLOWERING, FREQUENCY AND RELATIVE FREQUENCY OF FLOWERING FOR SPECIMENS OF *Clintonia borealis* IN AN OPEN SITE AND A CLOSED SITE

	Total Number of Plants	Number of Flowering Plants	Percent Flowering	Frequency of Flowering	Relative Frequency of Flowering
Open Site	634	62	9.8	20	0.36
Closed Site	449	8	1.8	7	0.13

DISCUSSION

The results indicate clearly that open sites do favour flower production in *Clintonia borealis* with open site quadrats approximately three times as productive as closed site quadrats. In addition, the percentage of flowering individuals was far greater for open sites than closed. However, field observations indicate that plants inhabiting open sites are far more likely to suffer frost injury early in the spring, resulting in damaged inflorescences or wilting of the entire aboveground components of the plant. It is therefore possible that the figures for percent flowering and relative frequency of flowering could have been even higher for open site quadrats.

POLLINATION MECHANISMS

An experiment to identify the mechanism(s) of pollination of the flowers of Clintonia borealis was undertaken during the spring of 1978.

Sixty fertile plants growing under a mixed stand composed mainly of Picea mariana, Populus tremuloides and Betula papyrifera were located prior to the opening of flowers and treated as follows:

Group A:	untreated plants open to insect visits
Group B:	normal flowers enclosed within insect excluders
Group C:	emasculated flowers open to insect visits
Group D:	emasculated flowers enclosed within insect excluders
Group E:	normal flowers enclosed within insect excluders but cross-pollinated by hand
Group F:	emasculated flowers enclosed within insect excluders and cross-pollinated by hand.

The system of treatment is that of Kevan (1972) who applied it to the study of pollination mechanisms of several species of high arctic flowering plants. Only the three terminal flowers on each plant were utilized, since all others were removed so that results between treatments would be comparable.

The insect excluders were constructed using 6" x 6" zip-lock polyethylene bags and two 1/8" diameter welding rod eighteen inches long. One rod was inserted into the ground on either side of the plant so that enough distance existed between the upper portions of the rods to allow the polyethylene bag to be slipped over the flowers without actually contacting them. The bags, which had previously been perforated with approximately fifty 1 mm diameter holes to prevent moisture condensation within them, were sealed at their bottoms using the zip-lock closure. The closure allowed a tight seal to be made both around the support rods and the stipe.

Plants were emasculated, prior to opening of the flowers, using a pair of fine tweezers. No possibility of self-pollination existed prior to emasculation since anther dehiscence does not occur until after the flowers open.

The experiment was terminated on August 31, 1978. By this time, fruit development of treated plants was considered complete, with approximately eight weeks having passed since initiation of fruit development. Most berries, by this time, had the deep blue colouration typical of the ripened berries of untreated plants. The criterion used to establish whether successful fertilization of ovules had taken place was the presence of seeds within the fruit. In addition, the number of mature and partially mature seeds within each berry was taken as an indication of the success of fertilization for each particular treatment. Partially mature seeds, while the same size as mature seeds, were green instead of brown indicating that pigmentation of the seed coat had not yet occurred.

Relative success of pollination was calculated by dividing the total number of mature and partially mature seeds for each treatment by 3 (the number of flowers per stipe) and then by the number of plants exhibiting successful pollination for that particular treatment.

Absolute success of pollination was calculated by dividing the total number of mature and immature seeds for each treatment by 3 (the number of flowers per stipe) and then by 10 (the number of plants per treatment).

RESULTS

Table 24 is a comparison of the success of pollination between the six treatment groups for the population of Clintonia borealis under study.

Treatment A, which consisted of ten normal plants left open to insect visits, had one successfully pollinated plant and a total mature and partially mature seed count of 1. From Table 25 the relative and absolute success of pollination figures were 0.33 and 0.03 respectively.

Treatment B, which consisted of ten normal plants enclosed within insect excluders, had four successfully pollinated plants and a total mature and partially mature seed count of 14. From Table 25 the relative and absolute success of pollination figures were 0.17 and 0.47 respectively.

Treatment C, which consisted of ten plants with emasculated flowers open to insect visits, had three successfully pollinated plants and a total mature and partially mature seed count of 30. From Table 25 the relative and absolute success of pollination figures were 3.33 and 1.00 respectively.

Treatment D, which consisted of ten plants with emasculated flowers enclosed within insect excluders, had no successfully pollinated plants, therefore figures for total mature and partially mature seeds and relative and absolute success of pollination were all zero.

Treatment E, which consisted of ten plants with normal flowers enclosed within insect excluders but cross-pollinated by hand, had eight successfully pollinated plants and a total mature and partially mature seed count of 66. From Table 25 the relative and absolute success of pollination figures were 2.75 and 2.20 respectively.

Treatment F, which consisted of ten plants with emasculated flowers enclosed within insect excluders and cross-pollinated by hand, had eight successfully pollinated plants and a total mature and partially mature seed count of 289. From Table 25 the relative and absolute success of pollination figures were 12.04 and 9.63 respectively.

TABLE 24

A COMPARISON OF THE SUCCESS OF POLLINATION BETWEEN SIX DIFFERENT TREATMENTS FOR SPECIMENS OF *Clintonia borealis*

Treatment	Number Treated	Number Successfully Pollinated	Number Unsuccessfully Pollinated	Total Number of Mature Seeds	Total Number of Partially Mature Seeds*	Total Number of Mature and Partially Mature Seeds
A	10	1	9	1	0	1
B	10	4	6	12	2	14
C	10	3	7	4	26	30
D	10	0	10	0	0	0
E	10	8	2	58	8	66
F	10	8	2	289	0	289

* Partially mature seeds, while the same size as mature seeds, were green instead of brown, indicating that pigmentation of the seed coat had not yet occurred.

TABLE 25

A COMPARISON BETWEEN THE RELATIVE AND ABSOLUTE SUCCESS OF POLLINATION BETWEEN SIX DIFFERENT TREATMENTS FOR SPECIMENS OF *Clintonia borealis*

Treatment	Relative Success of Pollination	Absolute Success of Pollination
A	0.33	0.03
B	1.17	0.47
C	3.33	1.00
D	0	0
E	2.75	2.20
F	12.04	9.63

DISCUSSION

The study of the pollination mechanism of Clintonia borealis yielded some interesting results. From observations in the field it is known that insects, especially bees, do visit the flowers; however, the figures indicate that insect pollination is not the only method that Clintonia borealis employs. Utech (1973) has stated that the open floral structure of C. borealis indicates insect-mediated cross pollination as well as "a generalized faculative allogamy".

Treatment D, in which plants were emasculated and enclosed within insect excluders provided a check on the reliability of apparatus for keeping insects away from the flowers. Since no plants were fertilized in Treatment D, the results for all other treatments were considered valid. Relative success of fertilization takes into consideration only plants that were successfully fertilized and thus provides a measure of effectiveness for any given treatment for plants known to be capable of successful pollination. Absolute success of pollination considers all plants within a treatment and is therefore a measure of the effectiveness of that treatment on the population as a whole.

Plants in Treatment C are assumed to have been pollinated by insects because self pollination was not possible since these plants were emasculated. Plants in Treatment B could only have been self pollinated. Comparing these two groups with regard to relative success of pollination, Group C was approximately three times as successful as Group B. However, Group C was only twice as successful as Group B with respect to absolute success of pollination. What seems unusual, though, is that plants in Group A which were open to insect visits and capable of self pollination had relative and absolute success figures lower than both Groups B and C. Since the major pollination mechanism appears to be insect mediated, successful pollination becomes a function of the availability of suitable pollinators and the number of effective visits each plant receives.

Treatments E and F both involved cross pollination by hand of enclosed plants, Group E having normal flowers and Group F emasculated flowers. Because eight plants were successfully fertilized in each group but more seeds were produced by Group F, the relative and absolute success figures for F were 4.4 times as great as E. While the effectiveness of hand pollination, carried out by rubbing a dehisced anther across the surface of the open stigma, may be questioned, emasculation may have some unexplained positive effect on stigma receptiveness. As previously noted, Treatment C with emasculated flowers was more successfully pollinated than Group A with normal flowers.

The results do indicate that the flowers of Clintonia borealis are pollinated primarily by insects but that the plant possesses a capacity for self pollination. If the experiment was repeated, one additional treatment would be added, consisting of normal plants enclosed within insect excluders but self pollinated by hand.

BERRY VOLUME AND
SEED NUMBER RELATIONSHIPS

Observation of berry size and seed number made on the specimens of Clintonia borealis used in the pollination study (see previous section) led the author to speculate that there may be a link between the size of the berry and the number of mature seeds that it contains. In general, large berries seemed to contain the most mature seeds, and so to test the existence of a relationship a random collection of fruit was made so that measurements of berry size and seed number could be taken. Utech (1973) has already determined that the average number of ovules/gynoecium for C. borealis is 16.8.

Fruit for the study, collected during September 1978, came from two populations, one on the campus of Lakehead University and the second located at an approximate distance of 20 km from the campus. No distinction was made between berries collected from each site.

Using a pair of dividers, measurements were taken of the length and width of each berry, after which the berry was dissected and the seeds removed. A count was then taken of mature and partially mature seeds in each berry, partially mature seeds being virtually the same size as mature seeds but lacking a brown pigmented seed coat. Any other seeds that may have been present were disregarded, since those seeds were of a much smaller size than mature or partially mature seeds and would have contributed an insignificant amount toward the volume of the berry. In total 202 berries were examined.

In order to calculate the berry volume the shape of the berries was described in terms of one of two possible geometric figures.

The first, a prolate spheroid, described berries which were longer across the poles than across the middle, and the second, a sphere, described berries that had equal measurements across the poles and across the middle. The appropriate formula was then used to calculate the volume of each berry.

The formula for the volume of a prolate spheroid is

$$V = 4/3 \pi a \cdot b^2$$

where a = the length of the major semiaxis, and b = the length of the minor semiaxis and $\pi = 3.1416$.

The formula for the volume of a sphere is

$$V = 4/3 \pi r^3$$

where r = the radius from the centre.

An APL computer program was designed to handle the data upon which a statistical analysis was performed.

RESULTS

Table 26 lists the data collected on seed number and berry volume following the examination of 202 berries of *Clintonia borealis*.

Table 27 lists the statistical values yielded upon analysis of the data presented in Table 26 for the total of mature and partially mature seeds and berry volume. The maximum total number of seeds in the sample was 19 while the minimum was zero. The range in seed number was 19 and the mean 9.48. Variance and standard deviation was 19.95 and 4.47 respectively while median and mode were both 10.

For berry volume the maximum was 1488 mm^3 while the minimum was 78.54 for a range of 1410. Mean berry volume was 789.1 while variance and standard deviation were 9.11×10^4 and 301.8 respectively. The median was 823.6 and the distribution was bimodal being 831 and 980.2.

Tables 28 and 29 are the frequencies and relative frequencies of the numbers of mature, partially mature and total mature and partially mature seeds contained in the berries of *Clintonia borealis*.

Graph 1 is the smoothed curve of the relative frequencies of the total mature and partially mature seeds present in the berries examined.

Graphs 2 through 7 are the scatter diagrams and regression lines produced when berry volume is plotted against seed number. The R^2 value for mature, partially mature and total mature and partially mature seeds was 0.707, 0.097 and 0.825 respectively.

TABLE 26

FIGURES FOR THE NUMBER OF MATURE, PARTIALLY MATURE AND TOTAL MATURE AND PARTIALLY MATURE SEEDS, AND THE BERRY LENGTH, WIDTH AND VOLUME FOR THE FRUIT OF *Clintonia borealis*

Berry Number	Mature Seeds	Partially Mature Seeds	Total of Mature and Partially Mature Seeds	Length of Berry mm	Width of Berry mm	Volume of Berry mm^3
1	17	0	17	14	14	1437
2	19	0	19	13.5	12	1018
3	14	0	14	13	13	1150
4	10	0	10	13	11.5	900.2
5	11	3	14	12	12	904.8
6	0	0	0	13	12	980.2
7	5	0	5	11	11	696.9
8	11	0	11	12	11	760.3
9	14	0	14	13.5	12	1018
10	4	0	4	11	9	466.5
11	8	0	8	10	10	523.6
12	16	0	16	14	12.5	1145
13	17	0	17	14	12.5	1145
14	0	0	0	7	5	91.63
15	6	0	6	12	11	760.3
16	13	0	13	14	12	1056
17	15	0	15	13	12	980.2
18	17	0	17	14	13	1239
19	13	0	13	14	13	1239
20	6	2	8	12.5	12	942.5
21	0	4	4	11	10	576
22	0	0	0	6	5	78.54
23	0	0	0	6	5	78.54
24	0	1	1	8	8	268.1
25	13	0	13	13	12	980.2
26	7	1	8	12	11.5	831
27	8	2	10	11	11	696.9
28	12	1	13	13	12	980.2
29	8	0	8	12	12	904.8
30	6	0	6	11	10	576
31	10	0	10	12	12	904.8
32	11	0	11	14	14	1437

Berry Number	Mature Seeds	Partially Mature Seeds	Total of Mature and Partially Mature Seeds	Length of Berry mm	Width of Berry mm	Volume of Berry mm^3
33	6	0	6	11	10	576
34	11	0	11	13.5	13	1195
35	14	0	14	13.5	13	1195
36	13	0	13	14	13	1239
37	9	1	10	12	11	760.3
38	17	0	17	14	14	1437
39	9	0	9	12	11.5	831
40	3	15	18	13	13	1150
41	9	1	10	12	12	904.8
42	9	0	9	12	11.5	831
43	7	4	11	15	11.5	1039
44	7	5	12	13	11	823.6
45	0	4	4	12	8	402.1
46	0	14	14	12	11.5	831
47	0	13	13	12.5	12	942.5
48	0	7	7	11	9	466.5
49	13	0	13	14	13.5	1336
50	4	1	5	10	10	523.6
51	12	1	13	11.5	11.5	796.3
52	13	1	14	14	13	1239
53	10	0	10	12	12	904.8
54	0	10	10	12	12	904.8
55	14	0	14	12	12	904.8
56	9	0	9	12.5	12	942.5
57	13	0	13	13	12	980.2
58	3	5	8	11	10.5	635
59	12	1	13	12.5	11	791.9
60	4	2	6	11	11	696.9
61	13	0	13	14	13	1239
62	7	0	7	14	11	887
63	11	1	12	13	12	980.2

Berry Number	Mature Seeds	Partially Mature Seeds	Total of Mature and Partially Mature Seeds	Length of Berry mm	Width of Berry mm	Volume of Berry mm^3
64	11	1	12	13	12.5	1064
65	5	0	5	11	10.5	635
66	11	0	11	13	12.5	1064
67	4	0	4	12	11	760.3
68	0	2	2	9	8	301.6
69	0	0	0	9	7.5	265.1
70	10	2	12	13	12.5	1064
71	10	0	10	12.5	12	942.5
72	9	0	9	12.5	12	942.5
73	4	7	11	13	12	980.2
74	11	0	11	11	11	696.9
75	5	0	5	9.5	9	402.9
76	5	0	5	11	10	576
77	3	1	4	11	8.5	416.1
78	1	0	1	9	8.5	340.5
79	6	0	6	10.5	9	445.3
80	17	0	17	14	14	1437
81	5	0	5	11	11	696.9
82	11	0	11	14	11.5	969.4
83	13	1	14	14	13	1239
84	12	1	13	13	13	1150
85	16	0	16	12.5	11.5	865.6
86	1	7	8	12.5	10.5	721.6
87	7	0	7	11	10.5	635
88	2	8	10	12	11.5	831
89	5	0	5	11	10	576
90	10	0	10	12	11	760.3
91	17	0	17	15	12	1131
92	2	0	2	9	8	301.6
93	1	8	9	13	11	823.6
94	11	0	11	12	12	904.8

Berry Number	Mature Seeds	Partially Mature Seeds	Total of Mature and Partially Mature Seeds	Length of Berry mm	Width of Berry mm	Volume of Berry mm^3
95	7	1	8	11	10.5	635
96	10	0	10	11.5	11.5	796.3
97	11	3	14	12.5	12	942.5
98	7	0	7	12.5	11.5	865.6
99	0	0	0	8.5	8	284.8
100	1	0	1	8	7.5	235.6
101	0	0	0	9.5	9	402.9
102	13	0	13	12	11.5	831
103	2	0	2	10	9	424.1
104	0	1	1	10	9.5	472.5
105	0	0	0	7.5	6	141.4
106	14	0	14	13	11.5	900.2
107	13	0	13	13.5	12.5	1104
108	17	0	17	14	11.5	969.4
109	16	0	16	14	14	1437
110	0	13	13	14	13	1239
111	0	14	14	14	12.5	1145
112	11	0	11	13	12	980.2
113	10	0	10	10	9.5	472.5
114	5	1	6	9	8	301.6
115	12	0	12	13.5	13	1195
116	10	0	10	13	12	980.2
117	19	0	19	14.5	14	1488
118	10	0	10	13	12	980.2
119	6	0	6	10.5	9.5	496.2
120	8	0	8	11	10	576
121	11	1	12	11.5	11	728.6
122	5	1	6	11	10.5	635
123	8	0	8	12	11.5	831
124	9	0	9	12.5	11	791.9
125	7	1	8	11	11	696.9

Berry Number	Mature Seeds	Partially Mature Seeds	Total of Mature and Partially Mature Seeds	Length of Berry mm	Width of Berry mm	Volume of Berry mm^3
126	6	0	6	13	11	823.6
127	9	1	10	12.5	10	654.5
128	7	0	7	12	10	628.3
129	6	0	6	11	9	466.5
130	16	0	16	12.5	11.5	865.6
131	15	0	15	15.5	12.5	1268
132	15	0	15	12.5	11.5	865.6
133	15	0	15	14	12	1056
134	10	0	10	13.5	12	1018
135	6	1	7	10.5	10	549.8
136	5	0	5	10	9	424.1
137	16	0	16	14	11	887
138	16	0	16	12	12	904.8
139	1	0	1	9	7.5	265.1
140	8	0	8	11	10	576
141	11	0	11	12.5	11	791.9
142	4	0	4	9.5	9.5	448.9
143	11	0	11	13	11.5	831
144	10	0	10	12	12	904.8
145	12	0	12	13.5	13	1195
146	12	0	12	12.5	12.5	1023
147	13	0	13	12.5	12	942.5
148	13	0	13	12.5	12	942.5
149	7	0	7	11.5	11	728.6
150	8	1	9	12	11	760.3
151	5	0	5	10	9.5	472.5
152	8	0	8	11	10.5	635
153	10	1	11	11	11	696.9
154	8	0	8	12	11	760.3
155	5	2	7	10	9.5	472.5
156	7	0	7	10	10	523.6

Berry Number	Mature Seeds	Partially Mature Seeds	Total of Mature and Partially Mature Seeds	Length of Berry mm	Width of Berry mm	Volume of Berry mm^3
157	13	0	13	15	13	1327
158	11	1	12	11.5	10.5	663.9
159	10	0	10	12	11	760.3
160	8	0	8	11	10.5	635
161	9	0	9	10	9	424.1
162	4	0	4	9	9	381.7
163	14	0	14	14	13	1239
164	12	0	12	11.5	11.5	796.3
165	14	1	15	13	12.5	1064
166	16	0	16	13.5	13	1195
167	6	0	6	13	11	823.6
168	9	0	9	11.5	11	728.6
169	15	0	15	13	11	823.6
170	11	0	11	11.5	10.5	663.9
171	11	0	11	12	11	760.3
172	13	0	13	12	11.5	831
173	10	0	10	11.5	10	602.1
174	3	0	3	9	8.5	340.5
175	10	0	10	10.5	10.5	606.1
176	2	0	2	8.5	8	284.8
177	13	0	13	13	13	1150
178	15	0	15	13	12	980.2
179	11	0	11	13.5	13	1195
180	9	0	9	11	11	696.9
181	9	0	9	14	12.5	1145
182	12	0	12	14	11	887
183	11	0	11	14	12	1056
184	13	1	14	13	11	823.6
185	10	0	10	12	11.5	831
186	5	0	5	10	10	523.6
187	5	0	5	9.5	9	402.9

Berry Number	Mature Seeds	Partially Mature Seeds	Total of Mature and Partially Mature Seeds	Length of Berry mm	Width of Berry mm	Volume of Berry mm^3
188	5	0	5	9	8.5	340.5
189	8	0	8	11	10	576
190	3	0	3	8.5	7.5	250.3
191	2	1	3	10	9	424.1
192	5	3	8	11	10	576
193	12	0	12	12	10	628.3
194	11	0	11	12	11	760.3
195	4	0	4	10	8.5	378.3
196	12	1	13	12	11.5	831
197	8	0	8	11.5	11	728.6
198	9	1	10	11.5	9.5	543.4
199	3	0	3	9	8.5	340.5
200	6	0	6	10.5	10	549.8
201	11	0	11	12	10	628.3
202	7	0	7	10.5	10	549.8

TABLE 27

STATISTICAL VALUES FOR THE TOTAL OF MATURE AND PARTIALLY MATURE SEEDS AND THE VOLUMES OF BERRIES OF *Clintonia borealis*

SEEDS

Sample Size	202 (number of berries examined)
Maximum	19
Minimum	0
Range	19
Mean	9.48
Variance	19.95
Standard Deviation	4.47
Median	10
Mode	10

BERRIES

Sample Size	202
Maximum	1488
Minimum	78.54
Range	1410
Mean	788.1
Variance	9.11×10^4
Standard Deviation	301.8
Median	823.6
Mode	831 980.2

TABLE 28

FREQUENCIES OF THE NUMBERS OF MATURE, PARTIALLY MATURE AND TOTAL MATURE AND PARTIALLY MATURE SEEDS CONTAINED IN THE BERRIES OF *Clintonia borealis*

Number of Seeds in Berry	Mature Seeds	Partially Mature Seeds	Total of Mature and Partially Mature Seeds
0	19	147	8
1	5	30	5
2	5	6	4
3	6	3	4
4	8	3	8
5	15	2	12
6	11	0	12
7	12	3	10
8	12	2	17
9	13	0	11
10	17	1	22
11	22	0	19
12	11	0	12
13	17	2	21
14	7	2	13
15	6	1	7
16	7	0	7
17	7	0	7
18	0	0	1
19	2	0	2

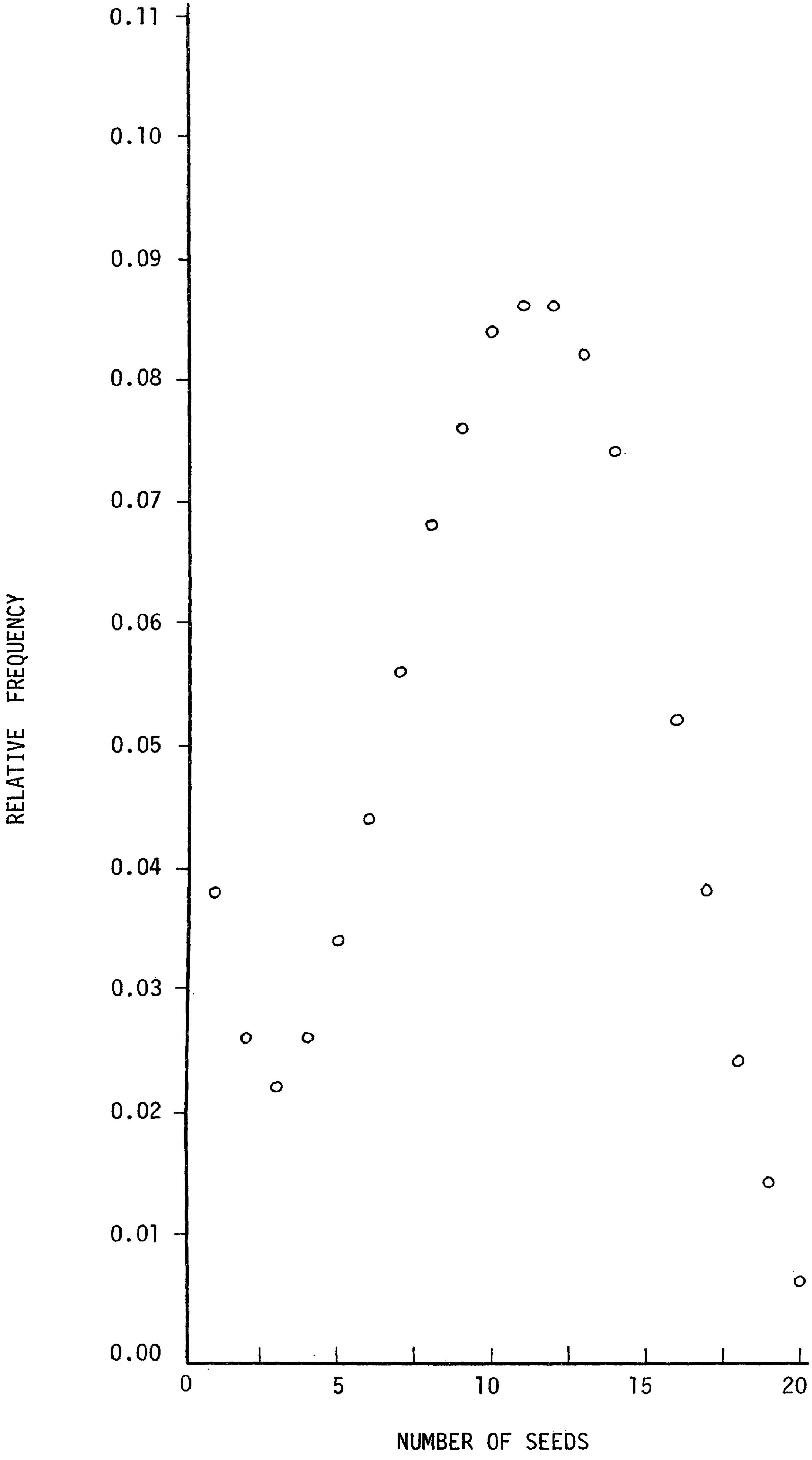
TABLE 29

RELATIVE FREQUENCIES OF THE NUMBERS OF MATURE, PARTIALLY MATURE AND TOTAL MATURE AND PARTIALLY MATURE SEEDS CONTAINED IN THE BERRIES OF *Clintonia borealis*

Number of Seeds in Berry	Mature Seeds	Partially Mature Seeds	Total of Mature and Partially Mature Seeds
0	0.094	0.728	0.040
1	0.025	0.149	0.025
2	0.025	0.030	0.020
3	0.030	0.015	0.020
4	0.040	0.015	0.040
5	0.074	0.010	0.059
6	0.054	0	0.059
7	0.060	0.015	0.050
8	0.060	0.010	0.084
9	0.064	0	0.054
10	0.084	0.005	0.109
11	0.109	0	0.094
12	0.054	0	0.059
13	0.084	0.010	0.104
14	0.035	0.010	0.064
15	0.030	0.005	0.035
16	0.035	0	0.035
17	0.035	0	0.035
18	0	0	0.005
19	0.010	0	0.010

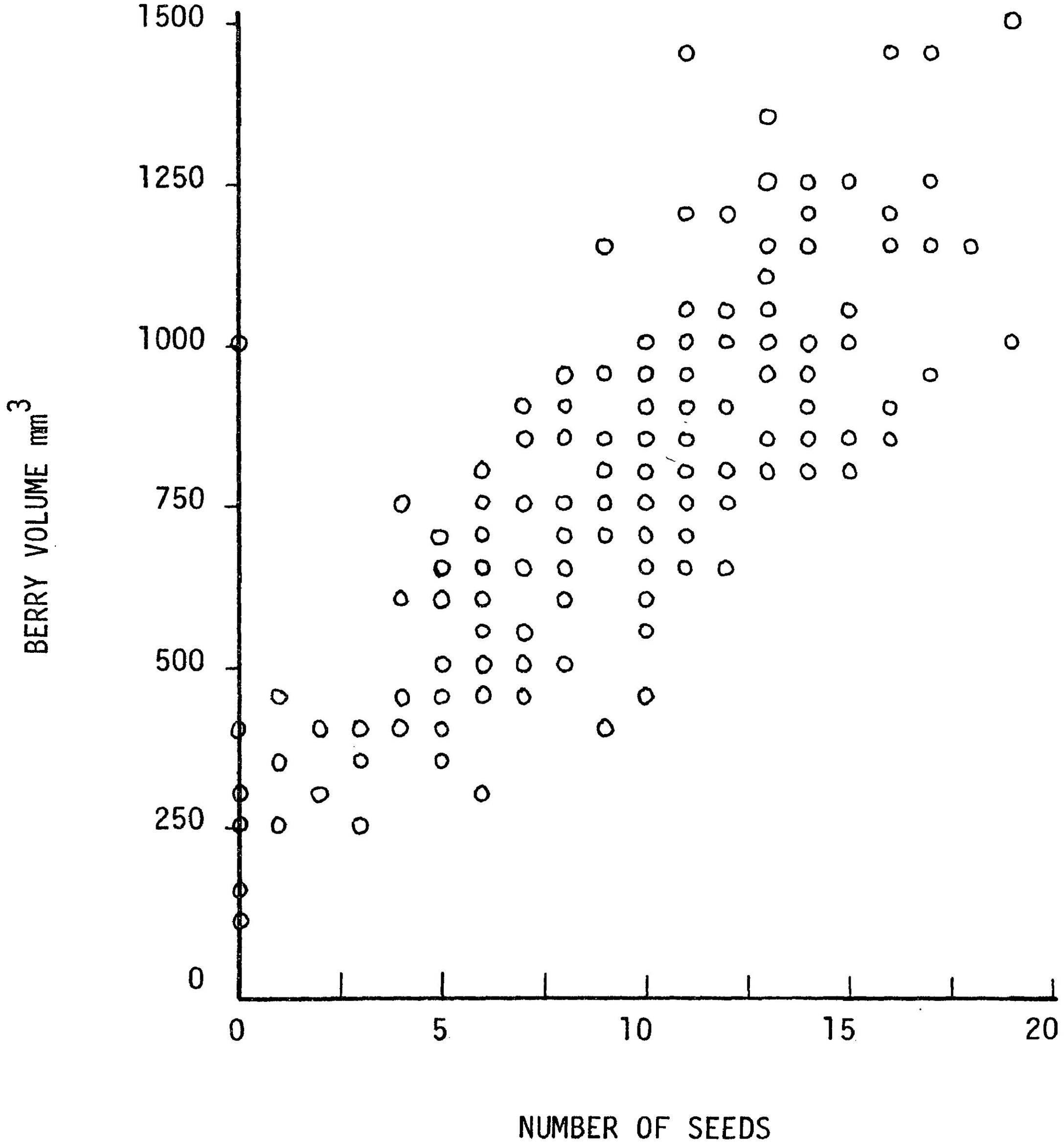
GRAPH 1

SMOOTHED CURVE OF RELATIVE FREQUENCY OF TOTAL OF MATURE AND PARTIALLY MATURE SEEDS COLLECTED FROM BERRIES OF *Clintonia borealis*


RELATIVE FREQUENCY
0.11
0.10
0.09
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0.00
0
5
10
15
20
NUMBER OF SEEDS

GRAPH 2

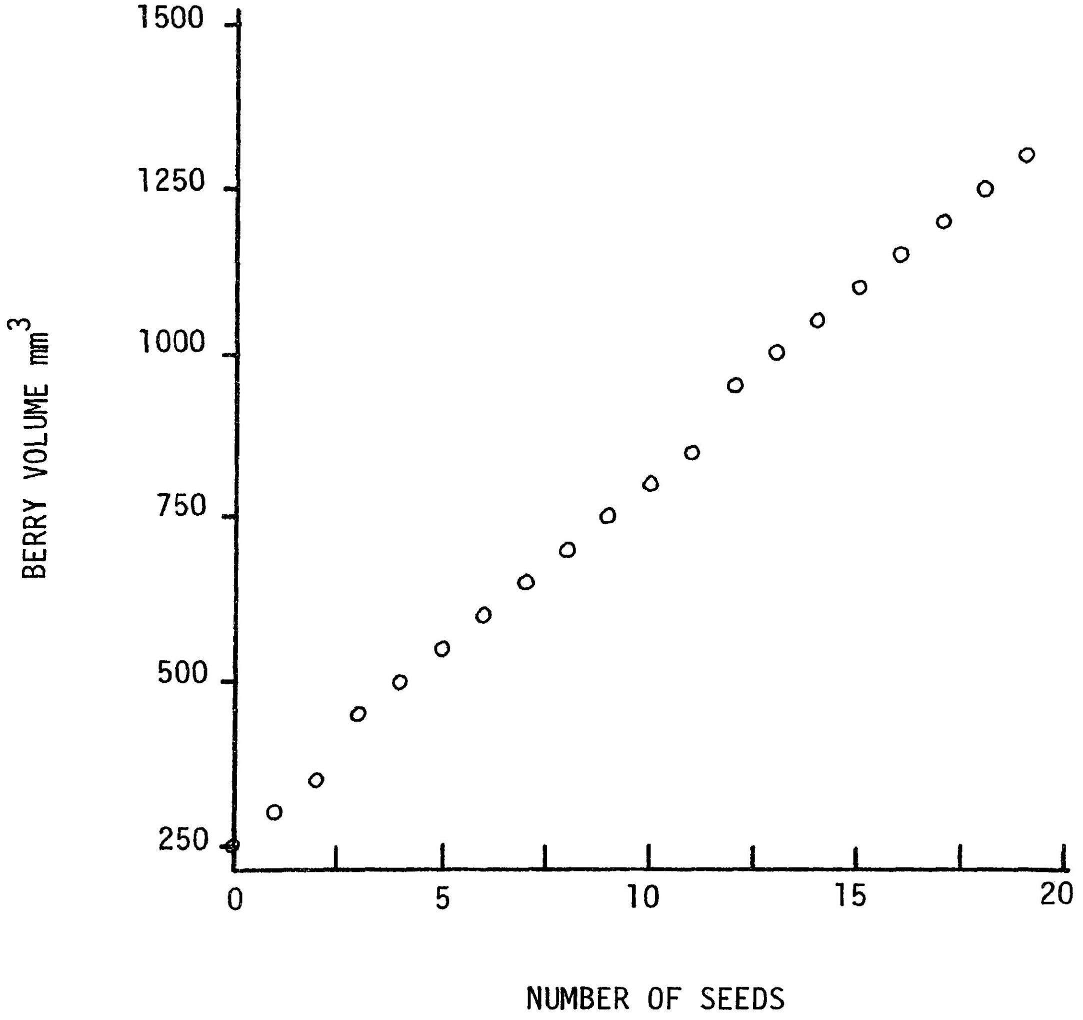
SCATTER DIAGRAM OF BERRY VOLUME VERSUS TOTAL MATURE AND PARTIALLY MATURE SEEDS


1500
1250
1000
750
500
250
0
BERRY VOLUME mm^3
0
5
10
15
20
NUMBER OF SEEDS

GRAPH 3

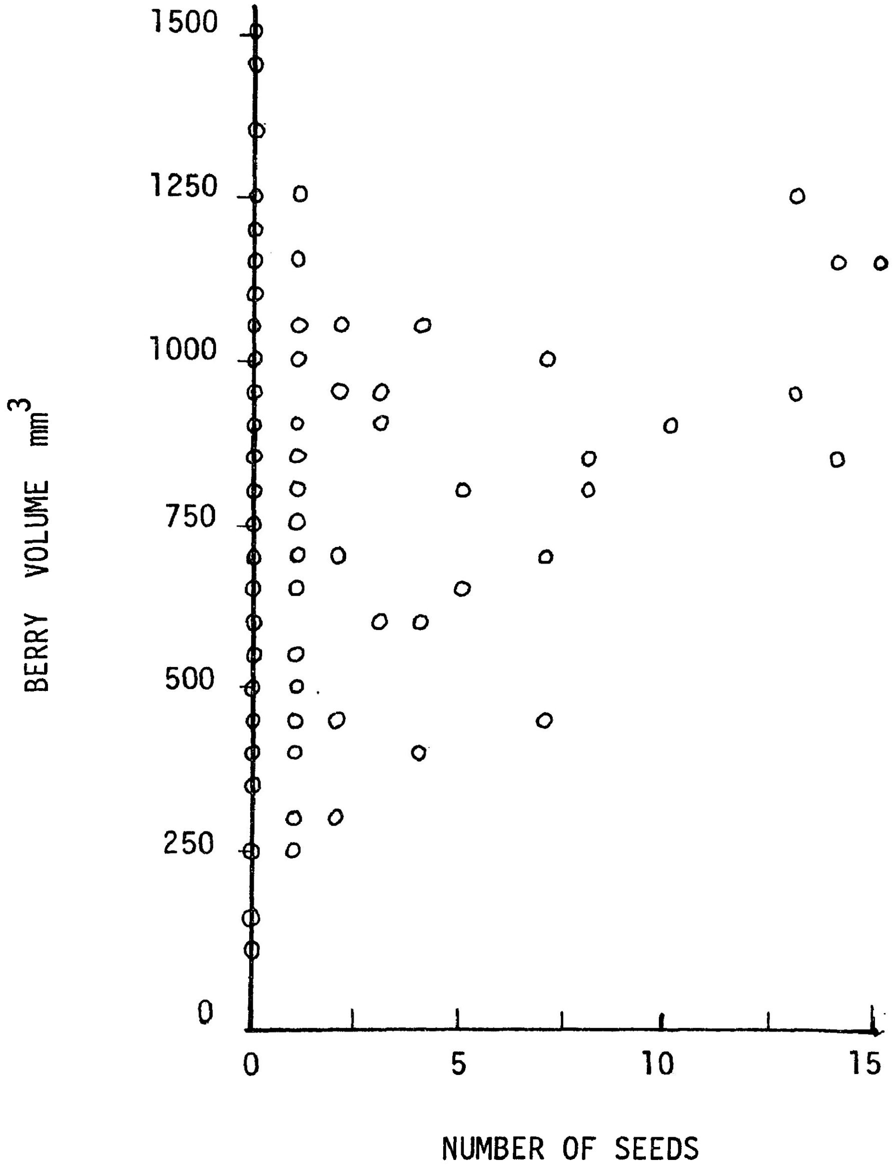
REGRESSION LINE OF BERRY VOLUME VERSUS TOTAL MATURE AND PARTIALLY MATURE SEEDS

$R^2 = 0.825$


1500
1250
1000
750
500
250
BERRY VOLUME mm^3
0
5
10
15
20
NUMBER OF SEEDS

GRAPH 4

SCATTER DIAGRAM OF BERRY VOLUME VERSUS NUMBER OF PARTIALLY MATURE SEEDS

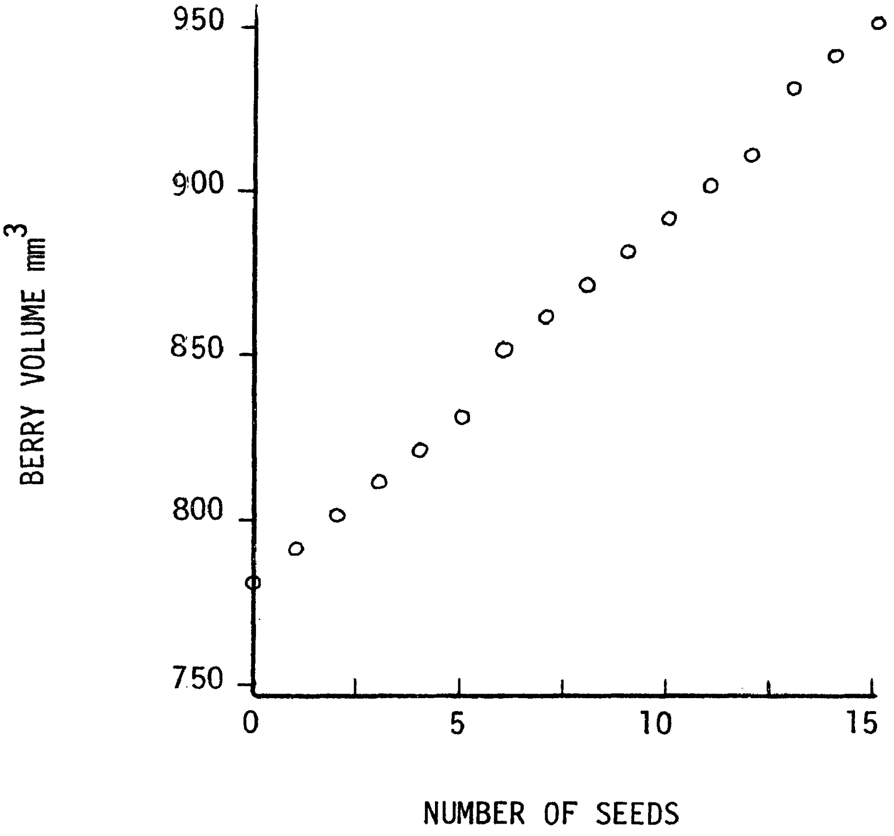

1500
1250
1000
750
500
250
0
BERRY VOLUME mm^3
0
5
10
15
NUMBER OF SEEDS

GRAPH 5

REGRESSION LINE OF BERRY VOLUME VERSUS

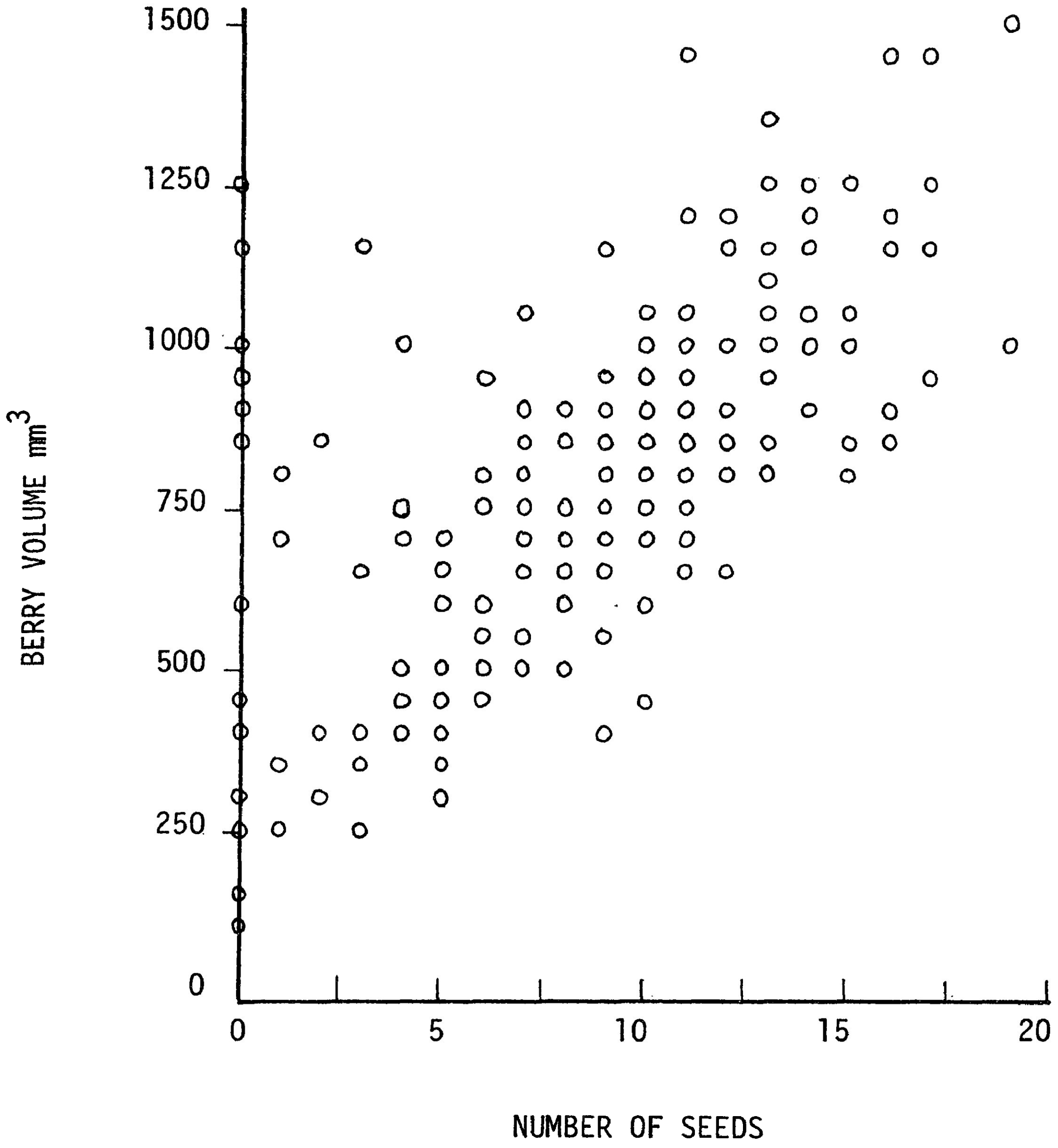
NUMBER OF PARTIALLY MATURE SEEDS

$R^2 = 0.097$


950
900
850
800
750
BERRY VOLUME mm^3
0
5
10
15
NUMBER OF SEEDS

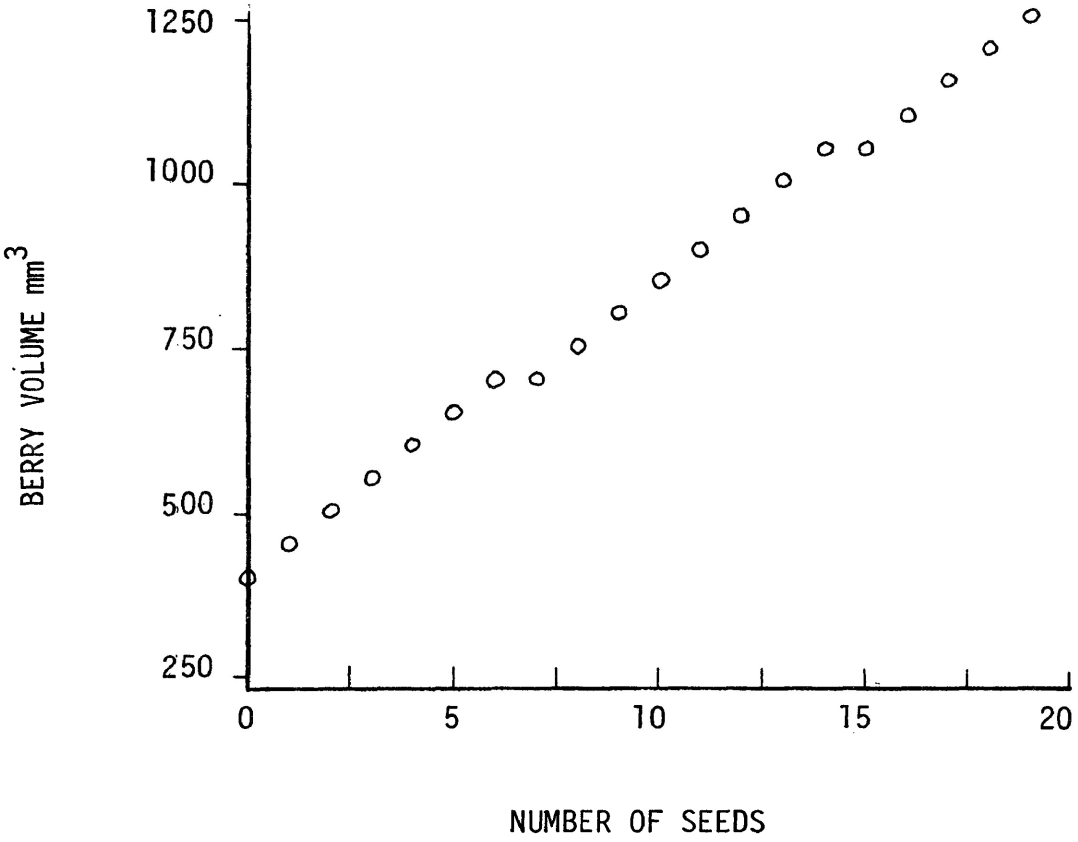
GRAPH 6

SCATTER DIAGRAM OF BERRY VOLUME VERSUS NUMBER OF MATURE SEEDS


1500
1250
1000
750
500
250
0
BERRY VOLUME mm^3
0
5
10
15
20
NUMBER OF SEEDS

GRAPH 7

REGRESSION LINE OF BERRY VOLUME
VERSUS NUMBER OF MATURE SEEDS
$R^2 = 0.707$


1250
1000
750
500
250
BERRY VOLUME mm3
0
5
10
15
20
NUMBER OF SEEDS

DISCUSSION

Results of the examination of 202 berries of Clintonia borealis revealed a definite correlation between berry volume and the number of seeds it contained. The R^2 value yielded through regression analysis indicated a very strong correlation when volume was compared to the total number of mature and partially mature seeds present ($R^2 = 0.825$). The closer the R^2 value is to 1 the stronger the correlation. A good correlation also existed between volume and the number of mature seeds present ($R^2 = 0.707$) but the correlation between berry volume and the number of partially mature seeds was weak ($R^2 = 0.097$). This no doubt stemmed from the fact that greater than 70 percent of the berries examined had zero partially mature seeds.

The significance of the correlation between berry volume and seed number is that the plant channels its energy reserves into the production of fruit in direct proportion to the numbers of mature seeds that are produced. This reproductive strategy makes sense if animal vectors are responsible for seed dispersal since large berries are likely to be more attractive and the ones most often eaten. It would be wasteful for the plant to channel energy into the production of a desirable fruit that contained no mature seeds since no seedlings could ever result. For Clintonia borealis total mature and partially mature seed numbers of nine to ten and berry volumes of 800 to 1000 mm^3 should be considered typical.

BIBLIOGRAPHY

Anderson, R. C. and O. L. Louck. 1973. Aspects of the biology of *Trientalis borealis* Raf. Ecol. 54 (4): 798-808.

Billings, W. D., P. J. Godfrey and R. D. Hillier. 1965. Photoperiodic and temperature effects on growth, flowering, and dormancy of widely distributed populations of *Oxyria*. Bull. Ecol. Soc. Amer., 46: 189.

Coombe, D. E. 1957. The spectral composition of shade light in woodlands. J. Ecology 45: 823-830.

Cooper, A. J. 1973. Root Temperature and Plant Growth - A Review. Research Review No. 4, Commonwealth Agricultural Bureaux, England.

Curtis, J. T. 1959. The Vegetation of Wisconsin. An Ordination of Plant Communities. Univ. Wisconsin Press, Madison, Wisconsin.

Donart, G. B. 1969. Carbohydrate reserves of six mountain range plants as related to growth. J. Range Manage. 22: 411-415.

Donart, G. and C. Cook. 1969. Carbohydrate reserve content of mountain range plants following defoliation and regrowth. J. Range Manage. 23: 15-19.

Frye, D. M. 1977. A botanical inventory of Sandhill Woodlot, Ingham County III. Phenology Study. Mich. Bot. 16: 34-38.

Gunther, P. 1972. The Phenodynamics of *Clintonia borealis* (Ait.) Raf. and C. umbellulata (Michx.) Morong (*Liliaceae*) as Related to Their General Distributions. Ph.D. Thesis, Pennsylvania State University.

Hadley, E. B. and L. C. Bliss. 1964. Energy relationships of alpine plants on Mt. Washington, New Hampshire. Ecol. Monog. 34: 331-357.

Hall, I. V. 1955. Floristic changes following the cutting and burning of a woodlot for blueberry production. Can. J. Agric. Sci. 35: 143-152.

Hillman, W. S. 1964. The Physiology of Flowering. Holt, Rinehart and Winston, New York.

Kevan, P. G. 1972. Insect pollination of high arctic flowers. Jour. Ecol. 60: 831-847.

LaRoi, G. H. 1967. Ecological studies in the boreal spruce-fir forests of the North American Taiga. I. Analysis of the vascular flora. Ecol. Mono. 37:229-253.

Linde, A., T. Janisch and D. Smith. 1976. Cattail - the significance of its growth, phenology and carbohydrate storage to its control and management. Dept. Nat. Res. Wis. Tech. Bull. No. 94.

Maclean, D. A. and R. W. Wein. 1977. Changes in understory vegetation with increasing stand age in New Brunswick forests: species composition, cover, biomass, and nutrients. Can. J. Bot. 55: 2818-2831.

Mooney, H. A. and W. D. Billings. 1960. The annual carbohydrate cycle of alpine plants as related to growth. Amer. J. Bot. 47: 594-598.

Proebsting, E. L. 1957. The effect of soil temperature on the mineral nutrition of the strawberry. Proc. Am. Soc. Hort. Sci., 69: 278-281.

Salisbury, F. B. 1963. The Flowering Process. Permagon Press, Oxford.

Smith, D. 1969. Removing and analyzing total nonstructural carbohydrates from plant tissue. Wis. Agr. Exp. Stn. Res. Rep. 41: 1-11.

Utech, F. H. 1973. A Biosystematic Study of the Genus *Clintonia* Raf. (Liliaceae: Polygonatae). Ph.D. Thesis, Washington University.

Utech, F. H. and L. B. Thein. 1973. Chromosome numbers in *Clintonia borealis* (Liliaceae). Mich. Bot. 12: 122-128.

Utech, F. H. 1975. Biosystematic studies on *Clintonia* (Liliaceae: Polygonatae) III. Cytogeography, chromosome number and morphology of the North American species of *Clintonia* Raf. Cytologia 40, 765-786.

Werner, P. A. 1975. Predictions of fate from rosette size in T easel (*Dipscacus follonum* L.)