

The reproductive biology of boreal forest herbs. I. Breeding systems and pollination

SPENCER C. H. BARRETT AND KAIUS HELENURM¹

Department of Botany, University of Toronto, Toronto, Ont., Canada M5S 1A1

Received July 24, 1986

BARRETT, S. C. H., and HELENURM, K. 1987. The reproductive biology of boreal forest herbs. I. Breeding systems and pollination. *Can. J. Bot.* 65: 2036–2046.

Detailed observations and experimental studies of the reproductive biology of 12 boreal forest herbs were conducted over a 3-year period (1978–1980) in spruce–fir forests of central New Brunswick. The species examined were *Aralia nudicaulis*, *Chimaphila umbellata*, *Clintonia borealis*, *Cornus canadensis*, *Cypripedium acaule*, *Linnaea borealis*, *Maianthemum canadense*, *Medeola virginiana*, *Oxalis montana*, *Pyrola secunda*, *Trientalis borealis*, and *Trillium undulatum*. All taxa are insect-pollinated perennials and most exhibit clonal growth. Floral syndromes of the understory community are relatively unspecialized with many species possessing small white or green flowers. A total of 103 taxa of insects were collected from flowers during the 1979 season. *Bombus* spp. are the major pollinators of 5 of the 12 species. Syrphid flies, bee flies, and halictid and andrenid bees were also commonly observed. Controlled pollinations were undertaken to determine the breeding systems of herbs. Bagged, self-, cross- and open-pollinated treatments were used to investigate the capacity for self-pollination, compatibility status, and factors influencing fecundity in each species. A diversity of reproductive systems was revealed. Six species are completely dependent on insects for pollination, four species are weakly autogamous, one is strongly autogamous, and one appears to be apomictic. Comparisons of fruit-set and seed set from controlled self- and cross-pollinations indicate that four species are strongly self-compatible, one is dioecious, and the remainder display varying degrees of self-incompatibility. Despite this variation, outbreeding appears to be the most common reproductive mode. In several species there is evidence that low pollinator service limits fruit-set.

BARRETT, S. C. H., et HELENURM, K. 1987. The reproductive biology of boreal forest herbs. I. Breeding systems and pollination. *Can. J. Bot.* 65 : 2036–2046.

Des observations détaillées et des études expérimentales de la biologie de la reproduction de 12 plantes herbacées des forêts boréales ont été faites pendant trois ans (1978–1980) dans les forêts d'épinettes–sapins du Nouveau-Brunswick central. Les espèces étaient les suivantes : *Aralia nudicaulis*, *Chimaphila umbellata*, *Clintonia borealis*, *Cornus canadensis*, *Cypripedium acaule*, *Linnaea borealis*, *Maianthemum canadense*, *Medeola virginiana*, *Oxalis montana*, *Pyrola secunda*, *Trientalis borealis* et *Trillium undulatum*. Il s'agit dans tous les cas de taxons vivaces entomophiles, et pour la plupart, de taxons à croissance clonale. Les syndromes floraux de la communauté du sous-bois sont relativement non-spécialisés, plusieurs espèces ayant de petites fleurs blanches ou vertes. Un total de 103 taxons d'insectes ont été recueillis des fleurs au cours de l'année 1979. Les espèces de *Bombus* étaient les principaux pollinisateurs de 5 des 12 espèces. Les syrphidées, les bombylidées, les halictidées et les andrenidées étaient aussi communément observées. Des pollinisations contrôlées ont été effectuées dans le but d'établir le système reproducteur des herbacées. Divers traitements (ensachement, autopolinisation, pollinisation croisée et pollinisation ouverte) ont été utilisés pour étudier l'aptitude à l'autopolinisation, le statut de la compatibilité et les facteurs affectant la fécondité de chaque espèce. Toute une gamme de systèmes reproducteurs a été découverte. Six espèces étaient complètement dépendantes des insectes pour la pollinisation, quatre espèces étaient faiblement autogames, une était fortement autogame et une a semblé être apomictique. Des comparaisons de la nouaison chez les plantes auto- et allo-pollinisées ont indiqué que quatre espèces étaient fortement auto-compatibles, une s'est avérée dioïque et les autres ont montré divers degrés d'auto-incompatibilité. Malgré cette variation, l'exogamie semble être le mode de reproduction le plus commun. Chez plusieurs espèces il semble qu'un mauvais service de pollinisation restreint la nouaison.

[Traduit par la revue]

Introduction

The boreal forest covers extensive areas of the cool north temperate regions of North America and Eurasia and is composed primarily of different assemblages of coniferous trees (Hare 1954; La Roi 1967; Kornaš 1972; Rowe 1972). At its southern boundary in North America, the forest gives way to a mixture of various coniferous and broad-leaved deciduous trees (e.g., Maycock and Curtis 1960). Despite considerable variation in the species composition and vegetation structure of northern forests (e.g., Carleton and Maycock 1978, 1981), virtually all of the tree species exhibit uniform methods of pollination and seed dispersal. Anemophily (wind pollination) and anemochory (wind dispersal) predominate, a feature common to many cool temperate forests of the world (Regal 1982) and a striking contrast to tropical forests, where biotic influences are often closely involved with the reproductive biology of tree species (e.g., Bawa 1974; Ashton 1976; Zapata and

Arroyo 1978; Sobrevila and Kalin-Arroyo 1982; Baker *et al.* 1983; Bawa *et al.* 1985a, 1985b).

The herbaceous understory of the boreal forest is composed almost exclusively of perennial species, many of which are clonal and have showy floral displays and conspicuous, fleshy fruits. This suggests that animals play an important role in pollination and seed dispersal. To investigate this possibility we initiated a study of the reproductive biology of 12 common, widespread boreal forest herbs occurring in spruce–fir forests of central New Brunswick. The study was designed to provide basic descriptive information on the breeding systems, pollination biology, and phenology of understory herbs. Such information is important for the design of more detailed studies of the population biology of individual taxa and can also provide insights into the selective forces shaping reproductive adaptations at the community level.

In this paper we (i) provide quantitative estimates of reproductive traits associated with the breeding systems of herbs under study, (ii) by controlled pollinations conducted under field conditions, determine the compatibility status of species, their capacity for self-pollination, and whether natural levels of

¹Present address: Department of Biology, Washington University, St. Louis, MO, U.S.A. 63130.

fruit-set may be limited by pollen availability; and (iii) identify the major insect visitors to flowers and comment on their roles as pollinators. Following the presentation of results we evaluate some of the factors that are likely to influence the reproductive success of herbaceous plants occurring in the boreal forest.

Materials and methods

Study site

All field studies were conducted on two plots 3 km apart located on the property of R. Jonah, 5 km east of Doaktown, Northumberland County, central New Brunswick, from May to September 1978, 1979, and 1980. Vegetation at the two sites is composed of elements of boreal forest, and common species include *Picea rubens* Sarg., *Picea mariana* (Mill.) BSP., *Abies balsamea* (L.) Mill., *Pinus strobus* L., *Tsuga canadensis* (L.) Carr., *Thuja canadensis* L., *Populus tremuloides* Michx., with occasional *Larix laricina* (Du Roi) K. Koch, *Acer saccharum*, and *Betula alleghaniensis* Britton. The vegetation of the area is classified as Acadian Forest by Rowe (1972), where further details of the structure, species composition, and climate of the region are available.

The two plots were approximately 1000 m² and were chosen because their understory vegetation was representative of the surrounding spruce–fir forests and each contained sufficient numbers of the 12 common boreal forest herbs under study to allow experimental studies. The 12 species comprised >95% of the herbaceous cover at each site. Other species of low frequency at the sites were *Gaultheria procumbens*, *Moneses uniflora*, and *Monotropa hypopitys*. The average frequency of the 12 herbs in the two plots was estimated by recording the number of times a given species occurred in twenty-five 1-m² quadrats positioned at random within each plot. Because the results of studies conducted at both sites were similar, data from the two plots were pooled in analyses and data presentations.

Reproductive traits

Observations and measurements of reproductive traits for each species were made by sampling plants at random from the two study plots. Traits examined were flower colour, blossom type, number of flowers per inflorescence, pollen production, ovule number, seed weight, fruit weight, and reproductive effort. Estimates of pollen production involved 10 replicates of one to five unopened buds, depending on the amount of pollen produced per flower. Pollen counts were made using a haemocytometer, using the method of Lloyd (1965). Reproductive effort was estimated by sampling reproductive stems (ramets) of each species just prior to fruit maturity, drying the aboveground portion in an oven at 75°C for 3 days, and weighing the aboveground vegetative parts separately from reproductive structures. Reproductive effort in this study is defined as the percentage of aboveground dry weight allocated to reproductive structures per ramet. Means and sample sizes are given in Table 3.

Insect visitors

Observations of insect visitors to flowers were made throughout the 3-year study period. During summer 1979, insect visitors to flowers of each plant species were observed and collected at daily intervals, weather permitting. Sampling was not quantitative, but an attempt was made to make systematic collections of insects visiting each of the 12 species during their peak flowering period. Differences in the total number of individuals collected on each plant species provide a rough estimate of the level of visitation that each species received. All insects were pinned, mounted, and later sent to specialists for identification.

Breeding systems

Information on the breeding system of each species was obtained by controlled hand-pollinations and bagging experiments. Flowers were protected from insect visitors by the use of fine mesh nylon net (Bridal Temptation, eight strands per centimetre) that enclosed the entire inflorescence and were secured by drawstrings encircling the peduncle. For some species (e.g., *Oxalis montana*) visited by small

Coleoptera, several thicknesses of net prevented insects from entering bags. In species with inflorescences that were unable to support the weight of the net bags (particularly after rain), enclosures were made with wire or wooden frames to surround the entire plant with netting (*Cornus canadensis*, *Linnaea borealis*, *Maianthemum canadense*, *Medeola virginiana*, *Oxalis montana*, *Pyrola secunda*, *Trientalis borealis*), or net bags were supported by wire hooks (*Clintonia borealis* and *Trillium undulatum*).

To determine the dependence of each species on insect visitation for seed set, comparisons of fruit and seed production in bagged and open-pollinated flowers were made. Waxed jeweller's tags attached around the peduncle were used for marking individuals. To assess the compatibility relationships of each species, individual plants were self- and cross-pollinated. Emasculation was undertaken for all cross-pollinated flowers and plants in both treatments were bagged prior to the pollinations being applied. In some species with multiple-flowered inflorescences not all flowers within an inflorescence were used in cross-pollinations. Flowers not pollinated were excised from inflorescences. Because of the extensive clone size of many of the herbs under study a special effort was made in cross-pollinations to use pollen from conspecific patches occurring at least 10 m away from the pollen recipient. After controlled crosses plants were immediately rebagged to prevent pollen contamination and herbivory. Pollination treatments were conducted only on chasmogamous flowers of *Oxalis montana*.

Fruit-set and seed set data from the four pollination treatments (unmanipulated and bagged, self-pollinated, cross-pollinated, and open-pollinated) were compared statistically by chi-square tests, tests for equality of percentages based on the arcsin distribution (Sokal and Rohlf 1969), and Student's *t*-tests.

Results

Floral biology

The 12 species of boreal forest herb that were examined at the two study plots in central New Brunswick are all entomophilous (Table 1). Floral complexity varied among the species, ranging from the relatively simple unspecialized bowl-shaped flowers of *Oxalis montana* and *Trientalis borealis* to more structurally complex flowers as in the orchid *Cypripedium acaule*. Most floral syndromes were, however, relatively unspecialized. Most species display either uniformly white flowers or perianth parts with a combination of white with green or pink (Table 1). Blue, deep yellow, red, or orange flowers are rare or absent from the forest floor, although these floral colours are well represented in meadows and disturbed areas adjacent to the forest.

Insect visitors

Peak flowering of the most abundant species in the community was in June. Detailed phenological data for each species are presented in Helenurm and Barrett (1987). Visitation by insects to flowers of the 12 species varied greatly during the season. During cool or wet weather, particularly in May and June, no insects were observed on flowers for extended periods lasting for up to 7 consecutive days. The major insect visitors to flowers are listed in Table 1. A total of 552 insects comprising 103 taxa were collected from flowers during summer 1979. The mean number of insect taxa and individuals visiting each plant species was 14 and 46, respectively. Visitation levels to *Aralia nudicaulis*, *Cornus canadensis*, and *Maianthemum canadense* were relatively high in comparison with the remaining species. The former were among the most common at the study sites. Not all visitors were effective pollinators; those listed in Table 1 are considered likely pollinators based on observations of their foraging activities.

TABLE 1. Floral biology of 12 boreal forest herbs of central New Brunswick

	Flower colour	Blossom type ^a	Major insect visitors ^b	Peak flowering ^c	Frequency at study sites
<i>Aralia nudicaulis</i> (Araliaceae)	Green—white	Brush	Bumblebees, solitary bees, and syrphids	Early June	0.24
<i>Chimaphila umbellata</i> (Pyrolaceae)	Pink—white	Bowl	Bumblebees and staphylinid beetles	Late July	0.03
<i>Clintonia borealis</i> (Liliaceae)	Yellow—green	Bell	Bumblebees and solitary bees	Early June	0.61
<i>Cornus canadensis</i> (Cornaceae)	White	Brush	Bumblebees, solitary bees, beeflies, and syrphids	Mid-June	0.83
<i>Cypripedium acaule</i> (Orchidaceae)	White—pink	Gullet	Bumblebees?	Mid-June	0.02
<i>Linnaea borealis</i> (Caprifoliaceae)	Pink	Bell	Solitary bees and syrphids	Early July	0.55
<i>Maianthemum canadense</i> (Liliaceae)	White	Brush	Solitary bees, bee flies, and syrphids	Early June	0.92
<i>Medeola virginiana</i> (Liliaceae)	Green—red	Dish	Flies?	Late June	0.08
<i>Oxalis montana</i> (Oxalidaceae)	White	Bowl	Solitary bees and syrphids	Early July	0.12
<i>Pyrola secunda</i> (Pyrolaceae)	Green	Bowl	Bumblebees and solitary bees	Mid-July	0.06
<i>Trientalis borealis</i> (Primulaceae)	White	Bowl	Syrphids	Early June	0.45
<i>Trillium undulatum</i> (Liliaceae)	White	Bowl	Solitary bees	Late May	0.24

^aBased on blossom classification of Faegri and Van der Pijl (1971).^bFrom collections listed in Appendix 1.^cFrom quantitative data detailed in Helenurm and Barrett (1987).TABLE 2. Species of bumblebees (*Bombus* spp.) collected from flowers of boreal forest herbs during summer 1979 in central New Brunswick

	Bumblebees			
	<i>Bombus perplexus</i>	<i>Bombus ternarius</i>	<i>Bombus terricola</i>	<i>Bombus vagans</i>
<i>Aralia nudicaulis</i>	×		×	×
<i>Chimaphila umbellata</i>			×	×
<i>Clintonia borealis</i>		×	×	×
<i>Cornus canadensis</i>	×	×	×	×
<i>Cypripedium acaule</i>				×
<i>Linnaea borealis</i>				×
<i>Maianthemum canadense</i>				×
<i>Pyrola secunda</i>				×

^aNot observed on *C. acaule* but carrying pollinia.

Species of *Bombus* (bumblebees) were major pollinators of five species at the study sites and visited 8 of the 12 species (Table 2). On cool days they were frequently the only insects to be observed visiting flowers. Of the remaining insects collected from flowers, syrphids, bombyliids, and various solitary bees (e.g., halictids and andrenids) were most commonly observed. Despite long periods of observation no insects that might have been significant to the pollination of *Cypripedium acaule* and *Medeola virginiana* were recorded from these species during the 3-year period. Two queens of *Bombus vagans* were, however, collected from flowers of other plant species and were carrying pollinia of *Cypripedium acaule*. This suggests that they may play a role in the pollination of the species.

Floral traits

Quantitative measures of floral traits are presented in

Table 3. Inflorescence size varied among species, although most exhibited a relatively small number of flowers per inflorescence. Five species had, on average, either one or two flowers, and only three species possessed more than 20 flowers per inflorescence. In the dioecious *Aralia nudicaulis*, male inflorescences produce nearly twice as many flowers as female inflorescences (Barrett and Helenurm 1981). In *Oxalis montana*, two flower types are produced, cleistogamous and chasmogamous. Cleistogamous flowers were not examined in detail.

Pollen:ovule (P:O) ratios ranged from 58 in *Chimaphila umbellata* to 6291 in *Clintonia borealis* (Table 3). The relatively low P:O ratios of the two members of the Pyrolaceae (*Chimaphila umbellata* and *Pyrola secunda*) are mainly the result of the extremely large number of ovules produced in flowers of the two species (Table 3). The P:O ratio of *Linnaea*

borealis was calculated on the basis of one ovule per flower. No case of more than a single seed per fruit was recorded from the range of pollination treatments applied to the species including controlled cross-pollinations, so we assume that the remaining ovules are either nonfunctional or display fixed levels of abortion. By comparing ovule number per flower with the number of seeds per fruit in cross-pollinated flowers, an estimate of the number of functional and (or) nonaborted ovules per flower can be obtained. The seed:ovule ratios for species in which data are available are *Clintonia borealis*, 0.52; *Cornus canadensis*, 0.40; *Linnaea borealis*, 0.10; *Medeola virginiana*, 0.76; *Oxalis montana*, 0.72; and *Trientalis borealis*, 0.70.

Pollination experiments

Percentage fruit-set, mean seeds per fruit, and statistical comparisons of fruit and seed production following the four pollinations treatments are presented in Tables 4 and 5, respectively.

The exclusion of insect visitors to flowers of six species (*Aralia nudicaulis*, *Cornus canadensis*, *Cypripedium acaule*, *Medeola virginiana*, *Maianthemum canadense*, *Trientalis borealis*) resulted in virtually no seed formation, indicating that they are dependent on insects for pollination. In four species small amounts of seed were produced in undisturbed flowers (*Chimaphila umbellata*, *Clintonia borealis*, *Linnaea borealis*, *Oxalis montana*), indicating some automatic self-pollination. However, the seed set of bagged flowers in the four species was well below that of the plants in the remaining treatments, indicating a major role for insects as pollen vectors. Cleistogamous flowers in *Oxalis montana* are completely autogamous. Significant levels of seed production from bagged flowers were obtained in only two species (*Pyrola secunda*, *Trillium undulatum*), indicating that they are highly autogamous or apomictic. Although the latter condition seems unlikely for *Pyrola secunda*, the observations of Swamy (1948) and P. Kevan (unpublished data) on apomixis in *Trillium undulatum* suggest a role for this reproductive system in the New Brunswick populations.

Comparisons of fruit-set and seed-set data from controlled self- and cross-pollinations of *Cornus canadensis*, *Maianthemum canadense*, *Medeola virginiana*, and *Trientalis borealis* suggest that these species are highly self-incompatible. Self-pollinations generally resulted in little seed production in comparison with cross-pollinations (Table 4). Self-pollinations of the remaining species (with the exception of *Aralia nudicaulis*, which is dioecious) resulted in various amounts of seed, indicating self-compatibility.

Although *Clintonia borealis* is clearly self-compatible, cross-pollinations consistently resulted in higher amounts of fruit and seed production compared with that from self-pollinations. The reduced seed set from self-pollinations may have resulted from weak self-incompatibility and (or) post-zygotic abortion of developing embryos caused by inbreeding depression (see Galen *et al.* (1985) and Galen and Weger (1986) for further details). Flowers of *Clintonia borealis* are strongly protogynous, and under field conditions it is possible that, despite self-compatibility, clones are largely outcrossed.

A notable feature of the data from controlled cross-pollinations is the low level of fruit-set obtained in *Cornus canadensis* (21.5%) and *Maianthemum canadense* (12.5%). Although the values are significantly higher than those obtained from self-pollinations, they are considerably lower than cross-pollinations of the other species (Table 4). The low fecundity

TABLE 3. Reproductive attributes of 12 boreal forest herbs of central New Brunswick

	Flowers per inflorescence	Pollen grains per flower	Ovule number per flower	Pollen/ovule ratio	Seed weight (mg) $n = 20$	Fruit weight (mg)	Reproductive effort (%)
<i>Aralia nudicaulis</i>	75.2, 11.4 (120)	—	5.0, 0 (20)	5579, 1402	3.40, 2.0	108.8, 11.2 (8)	23.3, 8.9 (15)
♀	125.3, 29.6 (120)	27890, 7012	—	—	—	—	—
♂	3.9, 1.5 (166)	308800, 55110	5587.0, 1262 (10)	58, 18	<0.1	23.0, 4.4 (20)	15.7, 7.2 (22)
<i>Chimaphila umbellata</i>	3.6, 0.9 (225)	103500, 3417	16.7, 1.9 (10)	6291, 2445	4.70, 1.0	45.4, 28.0 (65)	24.3, 7.8 (21)
<i>Clintonia borealis</i>	25.2, 7.4 (50)	2559, 450	2.0, 0 (20)	1279, 225	6.8, 2.4	33.6, 15.2 (21)	23.2, 7.9 (21)
<i>Cornus canadensis</i>	1.0, 0 (209)	NR	NR	NR	<0.1	181.1, 54.3 (5)	55.9, 15.8 (5)
<i>Cypripedium acaule</i>	1.6, 0.5 (235)	3546, 585	10.4, 1.3 (38)	3546, 585	<0.1	0.5, 0.2 (20)	16.5, 6.1 (20)
<i>Linnaea borealis</i>	20.3, 4.3 (50)	6418, 1691	4.0, 0 (50)	1604, 422	9.0, 2.4	26.0, 9.8 (22)	46.0, 11.9 (22)
<i>Maianthemum canadense</i>	2.9, 1.5 (109)	51440, 12360	9.3, 3.7 (10)	6120, 2177	5.3, 1.3	28.2, 22.5 (45)	11.7, 7.0 (33)
<i>Medeola virginiana</i>	1.0, 0 (203)	13470, 3172	5.0, 0 (21)	2694, 634	0.8, 0.2	5.2, 1.1 (14)	16.8, 8.6 (19)
<i>Oxalis montana</i>	9.4, 2.7 (107)	289500, 64210	1439.0, 278 (10)	202, 37	<0.1	2.8, 0.8 (20)	35.3, 11.0 (24)
<i>Pyrola secunda</i>	1.2, 0.4 (198)	35870, 8922	12.0, 2.3 (10)	3097, 1104	0.4, 0.1	3.9, 1.5 (28)	5.6, 7.7 (27)
<i>Trientalis borealis</i>	1.0, 0 (496)	43850, 20370	37.2, 16.2 (10)	1190, 215	4.1, 0.7	161.2, 107.8 (22)	23.1, 9.0 (21)
<i>Trillium undulatum</i>							

NOTE: Values are the mean, standard deviation, and sample size in parentheses. NR, not recorded.

TABLE 4. Fruit-set and seed set following controlled pollination

	Bagged				Self-pollinated			
	No. of flowering stems	No. of flowers	% fruit-set	No. of seeds/fruit \pm SD (<i>n</i>)	No. of flowering stems	No. of flowers	% fruit-set	No. of seeds/fruit \pm SD (<i>n</i>)
<i>Aralia nudicaulis</i>	7	203	0	—	—	—	—	—
<i>Chimaphila umbellata</i>	55	260	10.8	NR ^a	22	44	75.0	NR
<i>Clintonia borealis</i>	81	247	28.3	4.6 \pm 4.4 (70)	69	168	72.0	3.7 \pm 3.1 (121)
<i>Cornus canadensis</i>	59	1777	1.5	1.0 \pm 0 (27)	28	347	0	—
<i>Cypripedium acaule</i>	5	5	0	NR	15	15	100.0	NR
<i>Linnaea borealis</i>	28	54	35.2	1.0 \pm 0 (19)	19	30	66.7	1.0 \pm 0 (20)
<i>Maianthemum canadense</i>	76	1082	0.3	1.0 \pm 0 (3)	14	166	0	—
<i>Medeola virginiana</i>	28	50	2.0	4.0 \pm 0 (1)	21	21	4.8	3.0 \pm 0 (1)
<i>Oxalis montana</i>	34	34	32.4	3.7 \pm 0.6 (11)	13	13	100.0	3.1 \pm 1.2 (13)
<i>Pyrola secunda</i>	29	223	63.2	NR	8	34	94.1	NR
<i>Trientalis borealis</i>	8	8	0	—	14	14	0	—
<i>Trillium undulatum</i>	48	48	95.8	27.3 \pm 14.3 (46)	17	17	100.0	29.2 \pm 20.4 (17)

^aNR, not recorded.

is unlikely the result of sampling error or faulty pollination technique. Sample sizes were large and ample pollen from distant clones was applied to stigmas. In both years the results of cross-pollinations for both species were similar. It is more likely that the low fecundity of these species is associated with postzygotic processes associated with resource limitation (see below).

In eight species (*Aralia nudicaulis*, *Clintonia borealis*, *Cornus canadensis*, *Cypripedium acaule*, *Medeola virginiana*, *Oxalis montana*, *Pyrola secunda*, *Trientalis borealis*) fruit-set was significantly higher in controlled cross-pollinations in comparison with natural levels of fruit-set (Table 5). In *Chimaphila umbellata*, *Linnaea borealis*, and *Maianthemum canadense*, although fruit-set was higher in the cross-pollinated treatment than in the open-pollinated treatment, the differences were not significant. Fruit-set and seed set values following cross-pollination of *Trillium undulatum* were significantly lower than the corresponding values from the open-pollinated treatment. Nearly twice as many seeds per fruit were produced in open-pollinated flowers in comparison with each of the three experimental treatments (Table 3). The difference is difficult to interpret but may be associated with the possible apomictic mode of reproduction in the species, the influence of multiple pollen donors on fecundity in open-pollinated flowers (see Schemske and Pautler 1984), or damage to flowers as a result of hand-pollinations.

Fecundity

The natural levels of fruit and seed production varied greatly among the species of boreal forest herbs that were examined. Few flowers of *Cornus canadensis*, *Cypripedium acaule*, and *Trientalis borealis* set fruit, whereas most flowers of *Aralia nudicaulis*, *Chimaphila umbellata*, *Clintonia borealis*, and *Trillium undulatum* produced fruit. These differences were found in both years. In 8 of the 10 species that were examined, the percentage fruit-set of flowers was significantly lower in 1979 than 1978 (Fig. 1). In *Cornus canadensis*, the reverse pattern occurred; maximum fruit-set was recorded in both years for *Trillium undulatum*, although it is worth noting that considerable predation of flowers and fruits was evident in the plants used for phenological studies reported in Helenurm and Barrett (1987). No fruits were produced by *Cypripedium acaule* in 1978, whereas two were recorded the following year.

Discussion

Most understory herbs of the boreal forest are perennial and many are long lived with well-developed clonal growth. Reproduction usually involves occasional episodes of seedling recruitment as a result of disturbance (e.g., fire, logging) followed by long periods of vegetative growth. Once individuals attain reproductive status, flowering and seed production occur regularly as long as local site conditions are favourable. Heavy shade, waterlogging, and the poor nutrient regime of soils can all reduce the flowering capacity of populations.

At our study sites, the 12 species chosen for study comprised most of the herbaceous cover and were common in spruce–fir forests throughout the region. Most of the species have widespread distributions throughout the boreal forest region of North America. Two species (*Medeola virginiana*, *Trillium undulatum*) are, however, more characteristic of mixed coniferous–deciduous forests of southern Canada and the United States. Several taxa (*Chimaphila umbellata*, *Linnaea borealis*, *Oxalis montana* (= *O. acetosella*), and *Pyrola secunda*) are known from boreal forest regions of Eurasia or have close relatives there (Kornaš 1972).

Although members of the herbaceous understory community in central New Brunswick share the perennial, clonal habit, they display a diversity of reproductive systems. These range from obligate outbreeding enforced by dioecism (*Aralia nudicaulis*) or physiological self-incompatibility (e.g., *Medeola virginiana*) through species with self-compatibility and presumably mixed mating systems (e.g., *Pyrola secunda*) to autogamy and possible apomixis (*Trillium undulatum*). Despite this variation the predominant reproductive mode appears to be outbreeding with insect pollinators playing a central role in regulating the levels of self- and cross-pollination in taxa with self-compatibility. Isozyme markers could be profitably used in boreal forest herbs to obtain quantitative estimates of the mating systems of individual species (Clegg 1980).

Surveys of pollen:ovule ratios in flowering plants indicate that they are associated with the breeding system of species (Cruden 1977). In general, outcrossers exhibit relatively high P:O ratios in comparison with species that display a high degree of self-fertilization. Comparison of P:O ratios of boreal forest herbs with values published in Cruden's survey is instructive in this regard. All species investigated, except *Chi-*

treatments of 12 boreal forest herbs of central New Brunswick

Cross-pollinated				Open-pollinated			
No. of flowering stems	No. of flowers	% fruit-set	No. of seeds/fruit \pm SD (<i>n</i>)	No. of flowering stems	No. of flowers	% fruit-set	No. of seeds/fruit \pm SD (<i>n</i>)
13	183	90.7	—	280	20905	70.9	—
13	24	75.0	NR	182	733	57.4	NR
55	82	86.6	8.6 \pm 4.7 (71)	291	1081	61.5	11.2 \pm 4.5 (252)
26	371	21.5	1.0 \pm 0 (80)	220	5782	10.7	1.0 \pm 0.1 (50)
5	5	100.0	NR	194	194	1.0	NR
12	18	66.7	1.0 \pm 0 (12)	256	374	51.3	1.0 \pm 0 (20)
9	72	12.5	NR	205	4141	7.1	1.5 \pm 0.7 (70)
18	21	95.2	7.1 \pm 4.3 (20)	125	383	25.6	3.6 \pm 3.4 (60)
11	11	100.0	3.6 \pm 0.8 (11)	145	145	35.2	3.5 \pm 0.8 (12)
9	45	100.0	NR	118	1115	53.2	NR
10	10	100.0	8.4 \pm 1.4 (10)	50	85	27.0	3.1 \pm 1.5 (23)
40	40	90.0	28.0 \pm 19.1 (36)	391	391	100.0	40.2 \pm 19.0 (57)

TABLE 5. Statistical comparisons of fruit-set and seed set following pollination treatments of 12 boreal forest herbs of central New Brunswick

	Self-pollinated versus cross-pollinated		Bagged versus open-pollinated		Cross-pollinated versus open-pollinated	
	% fruit-set	Seeds/fruit	% fruit-set	Seeds/fruit	% fruit-set	Seeds/fruit
<i>Aralia nudicaulis</i>	—	—	***	—	***	—
<i>Chimaphila umbellata</i>	NS	—	***	—	NS	—
<i>Clintonia borealis</i>	*	***	***	***	***	***
<i>Cornus canadensis</i>	***	—	***	NS	***	NS
<i>Cypripedium acaule</i>	NS	—	NS	—	***	—
<i>Linnaea borealis</i>	NS	NS	*	NS	NS	NS
<i>Maianthemum canadense</i>	***	—	***	NS	NS	—
<i>Medeola virginiana</i>	***	—	***	—	***	***
<i>Oxalis montana</i>	NS	NS	NS	NS	***	NS
<i>Pyrola secunda</i>	*	—	**	—	***	—
<i>Trientalis borealis</i>	***	—	***	NS	***	NS
<i>Trillium undulatum</i>	*	NS	**	***	***	**

NOTE: NS, not significant; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

maphila umbellata and *Pyrola secunda*, have P:O ratios that fall into his outcrossing classes (facultative xenogamy $\bar{x} = 796.6$, xenogamy $\bar{x} = 5859.2$). The P:O ratios of these two exceptions are more suggestive of facultative autogamy ($\bar{x} = 168.5$) or obligate autogamy ($\bar{x} = 27.7$). *Pyrola secunda* is moderately autogamous and *Chimaphila umbellata* is weakly autogamous. The low P:O ratios of these species may partly result from their extremely high ovule numbers per flower. Both produce capsules containing very large numbers of tiny seeds (Table 3), and it is possible that this feature makes the P:O ratios less indicative of their actual breeding system. Because of this, we feel that it is premature to attempt any interpretation of the breeding systems of these species. A similar difficulty arises in *Cypripedium acaule*, although in this case the complex floral mechanism prohibits self-pollination and the species is entirely dependent on insect pollinators for cross-pollination (Stoutamire 1967).

Peak flowering for most understory herbs in central New Brunswick is June (Helenurm and Barrett 1987). During this period, cool, wet weather is frequent and at our study sites little pollinator activity was observed. Under these conditions flowers receive few pollinator visits and fruit-set and seed set

may be reduced accordingly. Comparison of data from controlled cross-pollinations and open-pollinations has been used to investigate whether plant reproductive success is pollen limited (reviewed in Rathcke 1983; Willson and Burley 1983). In 8 of the 12 species examined, fruit-set following cross-pollinations is significantly higher than in open-pollinated flowers. However, interpretation of these findings is not straightforward since in six of the species, fewer flowers per inflorescence were used in the cross-pollinated treatment than in the open-pollinated treatment. This was done in some species because of the difficulties encountered in cross-pollinating all flowers with multiflowered inflorescences. This procedure could artificially inflate fruit-set values for the cross-pollinated treatment in species in which low resource levels and high abortion rates limit the number of fruits matured (see Stephenson 1981). Two observations are relevant to this problem. First, comparison of *total* fruit number per inflorescence (rather than percentage fruit-set) in the two pollination treatments can be used as a conservative test of whether fruit-set is pollinator limited, as long as inflorescences in the two treatments are selected at random. When this approach was adopted it was found that 3 of the 6 species with smaller samples for

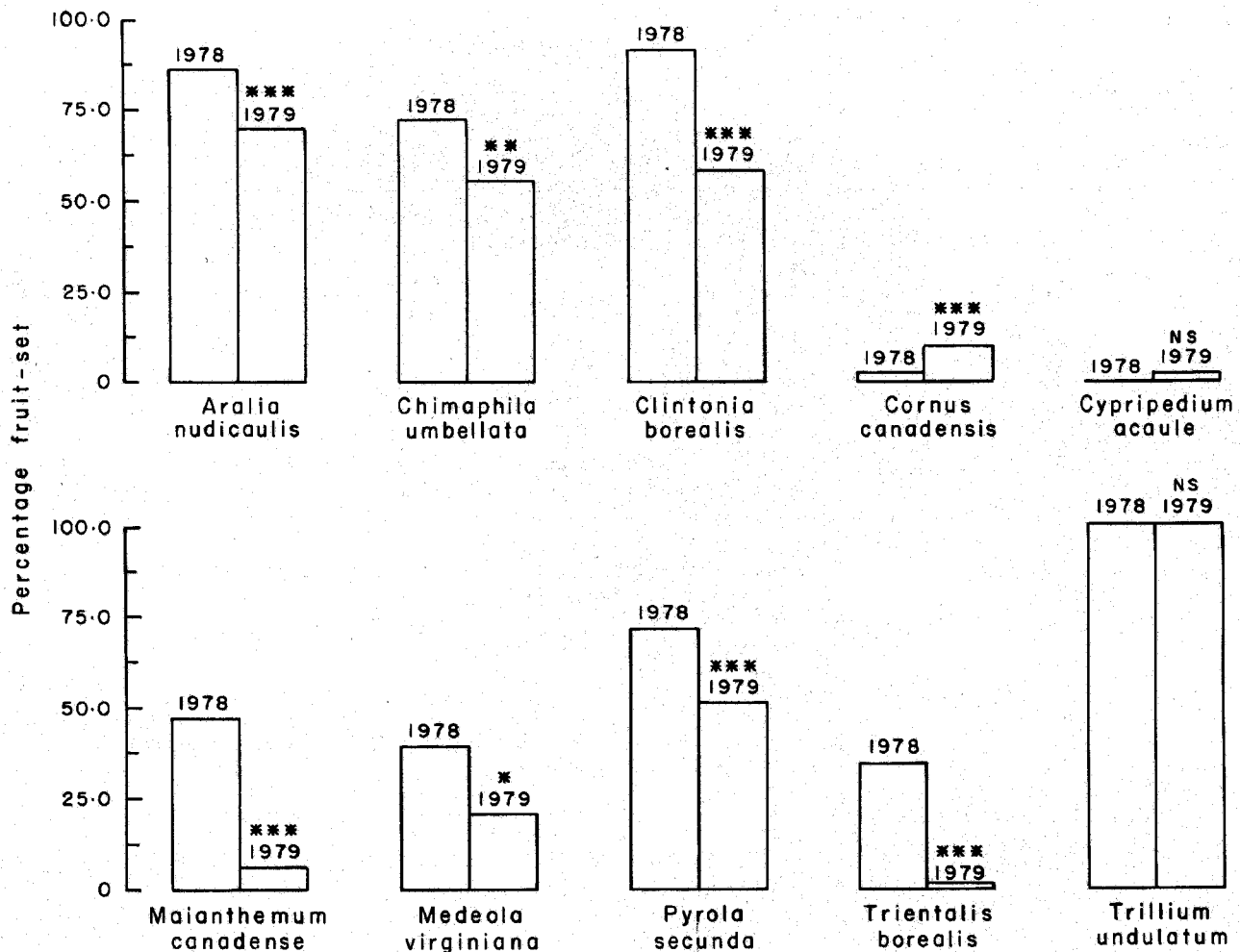


Fig. 1. Percentage fruit production in boreal forest herbs of central New Brunswick in 1978 and 1979.

cross-pollinated inflorescences (*Cornus canadensis*, *Medeola virginiana*, and *Trientalis borealis*) have significantly higher total fruit-set per inflorescence in this treatment in comparison with that from open-pollinated flowers. This indicates that, irrespective of the number of flowers used per inflorescence, cross-pollinations are capable of elevating fruit-set above that achieved in open-pollinated flowers.

The second observation concerns the frequency of fruit abortion in the species examined. If resource limitation largely restricts the percentage of fruits matured, this should be observable under field conditions. Our censuses of fruit development in 11 of the species indicated that in only 2 (*Cornus canadensis* and *Maianthemum canadense*) was there any significant degree of fruit abortion, suggesting that in these two species resources play a major role in regulating fruit-set (Helenurm and Barrett 1987).

Elsewhere, several authors have reported pollen limitation to fruit-set and seed set (Bierzzychudek 1981; Rathcke 1983). Although some controversy exists as to the interpretation of data (Bawa and Webb 1984; Garwood and Horvitz 1985), it seems generally agreed that the flowers of early flowering entomophilous species occurring in cool temperate climates may be prone to pollen limitation owing to reduced pollinator activity during inclement weather (Schemske *et al.* 1978). Since these species are frequently perennial, it is unlikely that fluctuations in pollinator numbers will have any dramatic effect on the overall fitness of individuals. Resources not used

for fruit and seed production within a given year may be reallocated to growth and flowering in later years.

The most striking examples of pollen limitation of fruit-set in our data occur in *Oxalis montana* and *Cypripedium acaule*. Plants of both species are self-compatible and controlled cross-pollinations yielded maximum fruit-set, while open-pollinated flowers produced no more fruits than did bagged flowers. Interpretation of these data is unambiguous because each species produces only a single flower per inflorescence, although *Oxalis montana* additionally produces cleistogamous flowers. No pollinators were observed visiting flowers of *Cypripedium acaule* during the 3-year period. A parallel study close to our study site of pollinium removal in *C. acaule* also provides evidence that these plants receive very little pollinator visitation. Of 236 flowers censused during 1979, only 26 had pollinia removed (Plowright *et al.* 1980). *Cypripedium acaule* is occasionally visited by bumblebees (Stoutamire 1967), but at our study site they largely concentrate their activities on other co-occurring species that flower at the same time as *C. acaule* (see Helenurm and Barrett 1987). Floral complexity and absence of nectar in the orchid presumably makes other species in the community more profitable food sources for bumblebees.

The five species showing pollen limitation (*Cornus canadensis*, *Cypripedium acaule*, *Medeola virginiana*, *Oxalis montana*, *Trientalis borealis*) may be indirectly affected to some extent by aerial spraying of insecticide for spruce bud-

worm control in New Brunswick. The effect of spraying on plant fecundity depends on the type of spray used, the time of flowering, and the insects that act as pollinators (Kevan 1975; Plowright *et al.* 1978; Kevan and La Berge 1979; Plowright and Rodd 1980; Thomson *et al.* 1985). Pollinator populations may be significantly reduced as a result of spraying, although recovery can occur later in the season. Several of the plant species we examined (*Aralia nudicaulis*, *Clintonia borealis*, *Cornus canadensis*, *Maianthemum canadense*) that flower immediately after spray applications in New Brunswick have been shown to have significantly lower fecundity in sprayed compared with unsprayed areas close to our study sites (Thaler and Plowright 1980). However, our plots were not in areas that were sprayed directly during the study period, and of the five pollen-limited species, only *Trientalis borealis* flowers at the time when pollinator populations are at their nadir. Nevertheless, since extensive insecticide spraying has been used for spruce budworm control in New Brunswick since 1952, it is possible that populations of pollinators are reduced over large areas despite absence of spraying at a local level over short time periods.

Since this study was completed, several of the understory herbs we examined have been investigated more intensively. As similar aspects of the reproductive biology were examined, it is worthwhile comparing the results and interpretations of these studies with our own. Anderson and Beare (1983) studied the breeding system and pollination ecology of *Trientalis borealis* in Michigan. They report three findings relevant to the present study: (i) the species is self-incompatible with 2.0% fruit-set upon selfing and 84.3% fruit-set in cross-pollinations; (ii) open-pollinated fruit-set averaged 66.1% and pollinator availability (halictid and andrenid bees) limits seed set; and (iii) the P:O ratio = 3,755. These results are in general agreement with our own but suggest that populations in New Brunswick may receive less pollinator service than those in Michigan. This may be associated with a reduced insect fauna caused by aerial spraying of insecticide over much of the province, as discussed previously. Further evidence to support this suggestion comes from a comparison of fruit-set data in *Oxalis montana*. Jasieniuk (1985) censused the fruit-set of chasmogamous flowers over a 2-year period (1980–1981) at five sites in Quebec. Her values average two to three times higher than the corresponding values for *Oxalis montana* in New Brunswick.

Galen *et al.* (1985) and Galen and Weger (1986) have recently reported on a detailed investigation of the pollination biology of *Clintonia borealis* in central Ontario. Their study shows that considerable variability in the strength of self-compatibility occurs among clones ranging from a high degree of self-compatibility to strong self-incompatibility. Similar patterns were evident in New Brunswick, suggesting that *C. borealis* possesses quantitative variation for self-incompatibility and (or) that the variation reflects different amounts of embryonic abortion of selfed zygotes as a result of inbreeding depression. A detailed analysis of the complete reproductive cycle in *Clintonia borealis*, from pollination to seed set, is required to distinguish between incompatibility phenomena and inbreeding depression. In the former case, we are dealing with a mechanism operating in maternal tissue and controlled by its genotype and that of the pollen or pollen donor. In contrast, inbreeding depression is a process acting in the progeny zygote determined by its own genotype. Although it is conceptually straightforward to distinguish between these factors,

in practice it may not always be clear which of these processes is responsible for the reduced seed set after selfing as opposed to outcrossing. Further discussion of the difficulties in distinguishing incompatibility phenomena from inbreeding depression are reviewed in Seavey and Bawa (1986) and Barrett (1987).

In addition to our own studies of dioecism in populations of *Aralia nudicaulis* from central New Brunswick (Barrett and Helenurm 1981; Barrett and Thomson 1982), Bawa *et al.* (1982) and Flanagan and Moser (1985) have investigated various aspects of the reproductive biology of this species in Massachusetts and Alberta, respectively. Flanagan and Moser (1985) provide evidence, based on controlled cross-pollinations, that at certain periods during the blooming period, inflorescences are pollen limited.

Amounts of fruit-set varied greatly among the 12 species that were examined. In general, values in 1979 were lower than in 1978. This may have been the result of unfavourable conditions for pollination and fruit maturation and (or) reduced pollinator visitation as a result of the spray programme. Unfortunately, quantitative information on pollinators was not collected and the meteorological information for the 2 years (see Helenurm and Barrett 1987) is not particularly informative. Comparison of fruit-set levels in the five obligately outbreeding herbs is of interest. Although *Aralia nudicaulis* had high percentage fruit-set in 1978 and 1979, the four self-incompatible species all displayed less than 50% fruit-set in both years (Fig. 1). All these species, with the exception of *Medeola virginiana*, flower during the same period, have small, white flowers, and are visited by similar pollinators. The high flower:fruit ratios of the self-incompatible species may result in part from selection for increased flower production to enhance pollen removal and male success (Willson and Burley 1983). According to this hypothesis, self-incompatible species maintain a significant number of flowers which function solely as males. However, females of dioecious species are not subject to these selective pressures and, as a result, a greater proportion of flowers may set fruit. Survey data of the fecundity of dioecious and self-incompatible species support this interpretation (Sutherland and Delph 1984) and it may help to explain the differences in fruit-set among some of the outbreeders observed in our study.

Acknowledgements

We thank Brenda Andrews, Sydney Cameron, Steven Falls, Lawrence Harder, Jim Grieshaber-Otto, Lester Hartling, Dave Maddison, Wayne Maddison, Robin Owen, Bruce Pendrel, Chris Plowright, Helen Rodd, Joel Shore, Gary Thaler, Barbara Thomson, and James Thomson for advice, technical assistance, and companionship during field studies in New Brunswick. Special thanks are extended to the Jonah family of Doaktown for providing living quarters and their forests for us to work in. We are grateful to the curatorial staff of the Royal Ontario Museum, Toronto, and Biosystematics Research Centre, Ottawa, for insect identifications, and Peter Kevan for comments on the manuscript. This research was funded by grants from the Natural Sciences and Engineering Research Council of Canada.

ANDERSON, R. C., and BEARE, M. H. 1983. Breeding system and pollination ecology of *Trientalis borealis* (Primulaceae). *Am. J. Bot.* 70: 408–415.

ASHTON, P. S. 1976. An approach to the study of breeding systems,

- population structure and taxonomy of tropical trees. In *Tropical trees: variation, breeding and conservation*. Edited by J. Burley and B. T. Styles. Academic Press, London. pp. 35–42.
- BAKER, H. G., BAWA, K. S., FRANKIE, G. W., and OPLER, P. A. 1983. Reproductive biology of plants in tropical forests. In *Ecosystems of the world*. 14A. Tropical rain forest ecosystems. Edited by F. B. Golley. Elsevier Scientific Publ. Co., Amsterdam. pp. 182–215.
- BARRETT, S. C. H. 1987. The evolution, maintenance and loss of self-incompatibility systems. In *Reproductive strategies of plants*. Edited by J. Lovett-Doust and L. Lovett-Doust. Oxford University Press, Oxford. In press.
- BARRETT, S. C. H., and HELENURM, K. 1981. Floral sex ratios and life history in *Aralia nudicaulis* (Araliaceae). *Evolution* (Lawrence, Kans.), **35**: 752–762.
- BARRETT, S. C. H., and THOMSON, J. D. 1982. Spatial pattern, floral sex ratios, and fecundity in dioecious *Aralia nudicaulis* (Araliaceae). *Can. J. Bot.* **60**: 1662–1670.
- BAWA, K. S. 1974. Breeding systems of tree species of a lowland tropical community. *Evolution* (Lawrence, Kans.), **28**: 85–92.
- BAWA, K. S., and WEBB, C. J. 1984. Flower, fruit and seed abortion in tropical forest trees: implications for the evolution of paternal and maternal reproductive patterns. *Am. J. Bot.* **71**: 736–751.
- BAWA, K. S., KEEGAN, C. R., and VOSS, R. H. 1982. Sexual dimorphism in *Aralia nudicaulis* L. (Araliaceae). *Evolution* (Lawrence, Kans.), **36**: 371–378.
- BAWA, K. S., PERRY, D. R., and BEACH, J. H. 1985a. Reproductive biology of tropical lowland rain forest trees. I. Sexual systems and incompatibility mechanisms. *Am. J. Bot.* **72**: 331–345.
- BAWA, K. S., BULLOCK, S. H., PERRY, D. R., COLVILLE, R. E., and GRAYUM, M. H. 1985b. Reproductive biology of tropical lowland rain forest trees. II. Pollination systems. *Am. J. Bot.* **72**: 346–356.
- BIERZYCHUDECK, P. 1981. Pollinator limitation of plant reproductive effort. *Am. Nat.* **117**: 838–842.
- CARLETON, T. J., and MAYCOCK, P. F. 1978. Dynamics of the boreal forest south of James Bay. *Can. J. Bot.* **56**: 1157–1173.
- . 1981. Understory–canopy affinities in boreal forest vegetation. *Can. J. Bot.* **59**: 1709–1716.
- CLEGG, M. T. 1980. Measuring plant mating systems. *BioScience*, **30**: 814–818.
- CRUDEN, R. W. 1977. Pollen:ovule ratios: a conservative indicator of breeding systems in flowering plants. *Evolution* (Lawrence, Kans.), **31**: 32–46.
- FAEGRI, K., and VAN DER PIJL, L. 1971. The principles of pollination ecology. 2nd ed. Pergamon, Oxford.
- FLANAGAN, L. B., and MOSER, W. 1985. Flowering phenology, floral display and reproductive success in dioecious *Aralia nudicaulis* L. (Araliaceae). *Oecologia*, **68**: 23–28.
- GALEN, C., and WEGER, H. 1986. Re-evaluating the significance of correlations between seed number and size: evidence from a natural population of the lily, *Clintonia borealis*. *Am. J. Bot.* **73**: 346–352.
- GALEN, C., PLOWRIGHT, R. C., and THOMSON, J. D. 1985. Floral biology and regulation of seed set and seed size in the lily *Clintonia borealis* (Ait.) Raf. *Am. J. Bot.* **72**: 1544–1552.
- GARWOOD, N. C., and HORVITZ, C. C. 1985. Factors limiting fruit and seed production of a temperate shrub, *Staphylea trifolia* L. (Staphyleaceae). *Am. J. Bot.* **72**: 453–466.
- HARE, F. K. 1954. The boreal conifer zone. *Geogr. Stud.* **1**: 4–18.
- HELENURM, K., and BARRETT, S. C. H. 1987. The reproductive biology of boreal forest herbs. II. Phenology of flowering and fruiting. *Can. J. Bot.* This issue.
- JASINIENIUK, M. 1985. Cleistogamy in *Oxalis montana* Raf. Ph.D. thesis, McGill University, Montréal.
- KEVAN, P. G. 1975. Forest application of the insecticide fenitrothion and its effect on wild bee pollinators (Hymenoptera: Apoidea) of lowbush blueberries (*Vaccinium* spp.) in southern New Brunswick, Canada. *Biol. Conserv.* **7**: 301–309.
- KEVAN, P. G., and LA BERGE, W. E. 1979. Demise and recovery of native pollinator populations through pesticide use and some economic implications. *Proceedings of the IVth International Symposium on Pollination*. Md. Agric. Exp. Stn. Spec. Misc. Publ. **1**: 489–508.
- KORNAŠ, J. 1972. Corresponding taxa and their ecological background in forests of temperate Eurasia and North America. In *Taxonomy, phytogeography and evolution*. Edited by D. H. Valentine. Academic Press, London. pp. 37–60.
- LA ROI, G. H. 1967. Ecological studies in the boreal spruce–fir forests of the North American taiga. I. Analysis of the vascular flora. *Ecol. Monogr.* **37**: 229–253.
- LLOYD, D. G. 1965. Evolution of self-compatibility and racial differentiation in *Leavenworthia* (Cruciferae). *Contrib. Gray Herb. Harv. Univ.* **195**: 3–134.
- MAYCOCK, P. F., and CURTIS, J. T. 1960. The phytosociology of boreal-conifer hardwood forests of the Great Lakes region. *Ecol. Monogr.* **30**: 1–35.
- PLOWRIGHT, R. C., and RODD, F. H. 1980. The effect of aerial insecticide spraying on hymenopterous pollinators in New Brunswick. *Can. Entomol.* **112**: 259–270.
- PLOWRIGHT, R. C., PENDREL, B. A., and McLAREN, I. A. 1978. The impact of aerial fenitrothion spraying upon the population biology of bumble bees (*Bombus* Latr: Hym.) in southwestern New Brunswick. *Can. Entomol.* **110**: 1145–1156.
- PLOWRIGHT, R. C., THOMSON, J. D., and THALER, G. R. 1980. Pollen removal in *Cypripedium acaule* (Orchidaceae) in relation to aerial fenitrothion spraying in New Brunswick. *Can. Entomol.* **112**: 765–769.
- RATHCKE, B. 1983. Competition and facilitation among plants for pollinators. In *Pollination biology*. Edited by L. Real. Academic Press, London. pp. 305–325.
- REGAL, P. J. 1982. Pollination by wind and by animals. *Annu. Rev. Ecol. Syst.* **13**: 497–524.
- ROWE, J. S. 1972. Forest regions of Canada. Canadian Forest Service, Department of the Environment, Ottawa, Ont., Publ. 1300.
- SEAVEY, S. R., and BAWA, K. S. 1986. Late-acting self-incompatibility in angiosperms. *Bot. Rev.* **52**: 195–219.
- SCHEMSKE, D. W., and PAUTLER, L. P. 1984. The effects of pollen composition on fitness components in a neotropical herb. *Oecologia*, **62**: 31–36.
- SCHEMSKE, D. W., WILLSON, M. F., MELAMPY, M. N., MILLER, L. J., VERNIER, L., SCHEMSKE, K. M., and BEST, L. B. 1978. Flowering ecology of some spring woodland shrubs. *Ecology*, **59**: 351–366.
- SOBREVIDA, C., and KALIN-ARROYO, M. T. 1982. Breeding systems in a montane tropical cloud forest in Venezuela. *Plant Syst. Evol.* **140**: 19–37.
- SOKAL, R. R., and ROHLF, F. J. 1969. *Biometry*. Freeman, San Francisco.
- STEPHENSON, A. G. 1981. Flower and fruit abortion: proximate causes and ultimate functions. *Annu. Rev. Ecol. Syst.* **12**: 253–279.
- STOUTAMIRE, W. P. 1967. Flower biology of the lady's-slippers (Orchidaceae: *Cypripedium*). *Mich. Bot.* **6**: 159–175.
- SUTHERLAND, S., and DELPH, L. F. 1984. On the importance of male fitness in plants. I. Patterns of fruit set. *Ecology*, **65**: 1093–1104.
- SWAMY, B. G. L. 1948. On the post-fertilization development of *Trilium undulatum*. *Cellule*, **52**: 7–14.
- THALER, G. R., and PLOWRIGHT, R. C. 1980. The effect of aerial insecticide spraying for spruce budworm control on the fecundity of entomophilous plants in New Brunswick. *Can. J. Bot.* **58**: 2022–2027.
- THOMSON, J. D., PLOWRIGHT, R. C., and THALER, G. R. 1985. Matacil insecticide spraying, pollinator mortality, and plant fecundity in New Brunswick forests. *Can. J. Bot.* **63**: 2056–2061.
- WILLSON, M. F., and BURLEY, N. 1983. *Mate choice in plants: tactics, mechanisms and consequences*. Princeton University Press,

Princeton.
ZAPATA, T. R., and ARROYO, M. T. K. 1978. Plant reproductive

ecology of a secondary deciduous tropical forest in Venezuela. *Biotropica*, 10: 221–230.

Appendix 1

The following are a list of insects collected from the flowers of boreal forest herbs at Doaktown, central New Brunswick, during May–August 1979. The number of individuals of each taxon caught is indicated in parentheses.

1. *Aralia nudicaulis* (Araliaceae); total taxa 17, total individuals 66
COLEOPTERA: Staphylinidae; *Eusphalerum convexum* Fvl. (7), *E. pothos* Mann (2), *Eusphalerum* spp. (31). Nitidulidae; *Cateretes* (Pullion) pennatus (Murray) (1). Cerambycidae; *Trachysida aspera brevifrons* (Howd.) (1). DIPTERA: Syrphidae; *Mallota posticata* Fab. (1), *Cheilosia tristis* Lw. (1). HYMENOPTERA: Apidae; *Bombus terricola* Kirby (2 queens), *B. perplexus* Cress. (3 workers), *B. vagans* Smith (8 queens). Halictidae; *Halictus rubicundus* (Christ.) (1), *Dialictus* spp. (1), *D. cressoni* (Rbstn.) (3), *D. imitatus* (Smith) (1), *Evylaeus quebecensis* (Cwfd.) (1). Andrenidae; *Andrena w-scripta* Vier. (1), *A. wheeleri* Graen (1)
2. *Chimaphila umbellata* (Pyrolaceae); total taxa 3, total individuals 70
DIPTERA: Milichiidae; *Paramyia nitens* Lw. (61). HYMENOPTERA: Apidae; *Bombus terricola* Kirby (4 workers), *B. vagans* Smith (4 workers, 1 male)
3. *Clintonia borealis* (Liliaceae); total taxa 15, total individuals 24
COLEOPTERA: Cerambycidae; *Pidonia ruficollis* (Say) (1). DIPTERA: Syrphidae; *Parasyrphus relictus* Zett. (2), *Carposcalis confusus* Cn. (1), *Sphaerophoria* sp. (1), Sarcophagidae; *Sarcophaga nearctica* Park (1). HYMENOPTERA: Apidae; *Bombus terricola* Kirby (3 queens), *B. vagans* Smith (6 queens), *B. ternarius* Say (2 queens). Halictidae; *Dialictus* sp. (1), *D. cressoni* (Rbstn.) (1), *D. imitatus* (Smith) (1), Andrenidae; *Andrena wilkella* (Kby.) (1). Megachilidae; *Osmia lignaria* Say (1). Crabronidae; *Rhopalum* sp. (1). LEPIDOPTERA: Noctuidae; *Poanes hobomok* (Harris) (1)
4. *Cornus canadensis* (Cornaceae); total taxa 65, total individuals 169
COLEOPTERA: Staphylinidae; *Eusphalerum pothos* Mann. (1). Cantharidae; *Cantharis* sp. (1). Elateridae; *Dalopius* sp. (1). Buprestidae; *Anthaxia expansa* LeC. (3). Cerambycidae; *Evodinus monticola monticola* (Rand.) (1), *Judolia montivagans montivagans* (Couper) (1), *Pidonia ruficollis* (Say) (8), *Acmaeopsoides rufula* (Hald.) (1). Chrysomelidae; *Orsodacne atra* (Ahrens) (1). Curculionidae; *Anthonomus* sp. (1), *Tychius stephensi* Schoer. (3). DIPTERA: Bombyliidae; *Bombylius major* L. (4), *Eclimius harrisi* (O.S.) (1). Syrphidae; *Mallota posticata* Fab. (1), *Parasyrphus relictus* Zett. (7), *Sphaerophoria longipilosa* Knut. (1), *S. bifurcata* Knut. (3), *Orthoneura pulchella* Will. (2), *Syrpitta pipiens* L. (1), *S. rectus* O.S. (1), *Tropidia quadrata* Say (2), *Blera confusa* John. (10), *B. badia* Walk. (1), *B. nigripes* Will. (1), *Temnostoma balyras* Walk. (3), *T. barberi* Cn. (2), *T. alternans* Lw. (1), *Cheilosia sialia* Shan (2), *Chalcosyrphus curvatus* Cn. (1), *C. inarmatus* Hunt (1), *C. memorum* Fab. (1), *C. nigra* Fab. (2), *Xylota bigelowi* Cn. (10), *X. hinei* Cn. (2), *Xylota* sp. (1). Muscidae; *Eudasyphora cyanicolor* (Zett.) (1), *Phaonia serva* (Meig.) (1). Milichiidae; *Paramyia nitens* Lw. (1). Sarcophagidae; *Sarcophaga nearctica* Park (1). HYMENOPTERA: Apidae; *Bombus terricola* Kirby (4 queens), *B. perplexus* Cress. (2 queens), *B. vagans* Smith (17 queens), *B. ternarius* Say (1 queen), *Psithyrus* sp. (1 queen). Colletidae; *Hylaeus basalis* Smith (1). Halictidae; *Halictus confusus* Smith (1), *Dialictus* spp. (17), *Evylaeus quebecensis* (Cwfd.) (7), *E. divergens* (Lovell) (1), *Sphecodes* spp. (2). Andrenidae; *Andrena melanochoa* Ckll. (3), *A. thaspis* Graen. (1), *A. rufosignata* Ckll. (1), *A. nivalis* Smith (2), *A. miranda* Smith (1), *A. sigmundi* Ckll. (1), *A. w-scripta* Vier. (7). Megachilidae; *Osmia proxima* Cress. (2). Anthophoridae; *Nomada sayi* Rbstn. (1). Eumenidae; *Ancistrocerus* spp. (2). Crabronidae; *Crabro* sp. (1). Tenthredinidae; *Zeraea americana* Cress. (1). LEPIDOPTERA: Pieridae; *Pieris napi* L. (1), *Celastrina argiolus lucia* (Kirby) (2). HEMIPTERA: Lygidae; *Lygus rufidorsus* (Kelton) (1)
5. *Cypripedium acaule* (Orchidaceae); total taxa 2, total individuals 8
COLEOPTERA: Staphylinidae; *Eusphalerum* spp. (6). HYMENOPTERA: Apidae; *Bombus vagans* Smith (2 queens)
6. *Linnaea borealis* (Caprifoliaceae); total taxa 21, total individuals 37
COLEOPTERA: Staphylinidae; *Eusphalerum* spp. (2). DIPTERA: Bombyliidae; *Eclimius harrisi* (O.S.) (3). Syrphidae; *Carposcalis confusus* Cn. (1), *Pyrophana rosarum* Fab. (1), *Sphaerophoria bifurcata* Knut. (1), *Sphaerophoria* sp. (1), *Melangyna lasiophthalma* Zett. (1). Muscidae; *Phaonia serva* (Meig.) (2), *Fannia unguata* Chill. (2). HYMENOPTERA: Apidae; *Bombus vagans* Smith (1 worker). Colletidae; *Hylaeus stevensi* Ckll. (1), *H. ellipticus* (Kby.) (5). Halictidae; *Dialictus* spp. (6), *D. cressoni* (Rbstn.) (1), *Evylaeus quebecensis* (Cwfd.) (3). Megachilidae; *Osmia proxima* Cress. (1), *O. pumila* Cress. (1). Crabronidae; *Crabro* sp. (1). Pemphredonidae; *Passaloecus* sp. (1). Tenthredinidae; *Zeraea americana* Cress. (1). LEPIDOPTERA: Noctuidae; *Euphyes vestris metacomet* (Harris) (1)
7. *Maianthemum canadense* (Liliaceae); total taxa 26, total individuals 85
COLEOPTERA: Staphylinidae; *Eusphalerum* sp. (1). Elateridae; *Agiotes stabilis* (LeC.) (2). DIPTERA: Bombyliidae; *Bombylius major* (L.) (3), *B. pygmaeus* (1). Syrphidae; *Parasyrphus relictus* Zett. (41), *Carposcalis confusus* Cn. (1), *Sphaerophoria* sp. (1), *Sphaerophoria bifurcata* Knut. (1), *Melangyna umbellatarum* Fab. (1), *Orthoneura pulchella* Will. (1), *Tropidia quadrata* Say (2), *Cheilosia slossonae* Shan. (1), *Xylota hinei* Cn. (1). Anthomyiidae; *Eremomyioides setosa* (Stein) (1), *Pegohylemyia fugax* (Mg.) (1). HYMENOPTERA: Apidae; *Bombus vagans* Smith (1 queen). Halictidae; *Halictus rubicundus* (Christ.) (1), *Dialictus* spp. (14), *D. cressoni* (Rbstn.) (3), *Evylaeus quebecensis* (Cwfd.) (1), *E. divergens* (Lovell) (1). Andrenidae; *Andrena nivalis* Smith (1), *A. miranda* Smith (1), Anthophoridae; *Nomada cuneata* (Rbstn.) (1). LEPIDOPTERA: Noctuidae; *Phalaenophana pyramusalis* Wlk. (1). HOMOPTERA: Cicadellidae; *Thamnotettix confinis* (Zett.) (1)
8. *Medeola virginiana* (Liliaceae); total taxa 1, total individuals 1
EPHEMEROPTERA: *Ephemerella* sp. (1)

9. *Oxalis montana* (Oxalidaceae); total taxa 6, total individuals 81
COLEOPTERA: Staphylinidae; *Eusphalerum convexum* Fvl. (1), *E. pothos* Mann. (11), *Eusphalerum* spp. (64).
DIPTERA: Syrphidae; *Melanostoma* sp. (2), *Cheilosia pallipes* Lw. (2). HYMENOPTERA: Halictidae; *Dialictus* sp. (1)
10. *Pyrola secunda* (Pyrolaceae); total taxa 4, total individuals 4
HYMENOPTERA: Apidae; *Bombus vagans* Smith (1 male). Halictidae; *Dialictus* sp. (1). Megachilidae; *Hoplitis producta* Cress. (1). Vespidae; *Vespula arenaria* Fabr. (1)
11. *Trientalis borealis* (Primulaceae); total taxa 3, total individuals 3
DIPTERA: Syrphidae; *Carposcalis confusus* Cn. (1), *C. obscura* Say (1), *Sphaerophoria bifurcata* Knut. (1)
12. *Trillium undulatum* (Liliaceae); total taxa 4, total individuals 4
COLEOPTERA: Buprestidae; *Anthaxia expansa* LeC. (1). DIPTERA: Syrphidae; *Carposcalis confusus* Cn. (1), *Sphaerophoria bifurcata* Knut. (1). HYMENOPTERA: Halictidae; *Dialictus* sp. (1)