

The reproductive biology of boreal forest herbs. II. Phenology of flowering and fruiting

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The flowering and fruiting phenologies of 12 boreal forest herbs were recorded during 1979 (flowering and fruiting) and 1980 (flowering only) in spruce–fir forests of central New Brunswick. The species studied 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*. Flowering in the community occurred from mid-May to the end of July. The order of flowering was maintained in the 2 years, but the degree of synchronization of inflorescences differed in several species. Fruiting in the community began in mid-July and extended beyond the end of September. The percentage of buds that ultimately bore fruit ranged from 0 (*Cypripedium acaule*) to 61% (*Aralia nudicaulis*). With the exception of *Cypripedium acaule*, which received little pollinator service, the self-incompatible species, *Cornus canadensis*, *Maianthemum canadense*, and *Medeola virginiana*, experienced the lowest levels of fruit-set. Pollen limitation and predation of developing fruit appear to be the major factors limiting percentage fruit-set in boreal forest herbs. Fruit production varied with time of flowering of inflorescences in several species, with periods of low fruit-set tending to coincide with lower densities of flowering inflorescences. Significant rates of fruit removal by herbivores occurred in all sarcochorous species. Disappearance of fruits from infructescences ranged from 31 (*Medeola virginiana*) to 95% (*Aralia nudicaulis*), with highest removal rates occurring during periods of greatest fruit availability.

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La phénologie florale et celle de la production des fruits de 12 plantes herbacées des forêts boréales ont été enregistrées au cours de 1979 (floraison et fructification) et 1980 (floraison seulement) dans les forêts d'épinettes-sapins du Nouveau-Brunswick central. Les espèces étudiées 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*. La floraison dans la communauté s'est faite de la mi-mai à la fin de juillet. L'ordre de floraison était maintenu durant les 2 années, mais le degré de synchronisation des inflorescences était différent chez plusieurs espèces. La fructification dans la communauté a commencé à mi-juillet et s'est poursuivie au-delà de la fin de septembre. Le pourcentage de bourgeons qui ont éventuellement porté des fruits allait de 0 (*Cypripedium acaule*) à 61% (*Aralia nudicaulis*). À l'exception du *Cypripedium acaule* qui a reçu peu de visites pollinisatrices, les espèces auto-incompatibles, *Cornus canadensis*, *Maianthemum canadense* et *Medeola virginiana*, ont connu les niveaux de nouaison les plus faibles. La restriction pollinique et le pillage des fruits en développement semblent être les facteurs principaux qui restreignent le pourcentage de nouaison chez les plantes herbacées des forêts boréales. La production de fruits a changé avec la période d'anthèse des inflorescences chez plusieurs espèces, les périodes où la nouaison était la plus faible ayant tendance à coïncider avec des densités inférieures d'inflorescences à fleurs épanouies. Des taux significatifs de vols de fruits par les herbivores ont été notés chez toutes les espèces à fruits charnus. La disparition des fruits des infrutescences allait de 31 (*Medeola virginiana*) à 95% (*Aralia nudicaulis*), les taux les plus élevés de pillage étant enregistrés durant les périodes où les fruits étaient les plus abondants.

[Traduit par la revue]

Introduction

Studies of the timing of reproductive events in flowering plant communities have been conducted in both tropical (Snow 1965; McClure 1966; Croat 1969; Daubenmire 1972; Frankie *et al.* 1974; Monasterio and Sarmiento 1976; Opler *et al.* 1976; Stiles 1977) and temperate (Mosquin 1971; Pojar 1974; Heinrich 1976; Schemske *et al.* 1978; Arroyo *et al.* 1981; Rabinowitz *et al.* 1981) regions. The examination of large numbers of species can aid in developing hypotheses concerned with the selective forces shaping community structure, although as Primack (1985) has pointed out, because of the interactive nature of abiotic and biotic factors, singling out the main environmental factors controlling reproductive patterns at the community level is a difficult task. At the least, community studies can provide basic descriptive information regarding the composition and structure of various communities in terms of

reproductive features and reveal interactions among species that merit more explicit experimental study.

The spruce–fir forests of central New Brunswick are part of the circumpolar boreal forest biome covering large areas of North America and Eurasia. The herbaceous understory of this forest (classified as Acadian Forest; Rowe 1972) has a relatively low diversity of species in comparison with many other plant communities. This feature permits detailed examination of patterns in the timing of reproductive events at the community level but, because species numbers are low, restricts statistical analysis of the correlates of pattern. Our study was designed to record the timing of flowering and fruiting for a large number of individuals of 12 common boreal forest herbs throughout the reproductive season in two consecutive years (1979–1980). This demographic approach to sexual reproduction, examining the same individuals throughout a reproductive season, also provides information regarding the fate of flowers and fruits that are produced.

The specific objectives of our study were (i) to document the flowering phenologies of boreal forest herbs, examine the dis-

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tribution of flowering times throughout the season, and compare the synchronization of flowering among species; (ii) to compare the flowering times of species in successive years and assess the constancy of this trait; (iii) to record fruiting phenologies and examine the distribution of fruiting times of the different species; and (iv) to document levels of fruit production and removal rates of fruits of boreal forest herbs. In a companion paper (Barrett and Helenurm 1987) the floral biology, breeding systems, and pollinators of the herbs studied here are described.

Materials and methods

Sites and sampling

Two study sites (3 km apart) in a spruce–fir forest near Doaktown, central New Brunswick, were used for studies of the phenology of flowering and fruiting in boreal forest herbs. Details of the location, vegetation, and species composition of the sites are given in Barrett and Helenurm (1987). Monthly temperature and rainfall data for the 3 years that the study was conducted (see Barrett and Helenurm, 1987, for data from 1978) were obtained from the Environment Canada Atmospheric Environmental Service meteorological station at Doaktown. Most sampling was undertaken using transects. Five transects 50 m in length were used at each site. The width of transects varied depending on flowering density. The transects were 1 m wide for the most abundant species (*Clintonia borealis*, *Cornus canadensis*, *Maianthemum canadense*, *Trientalis borealis*) but were expanded to 10 m for *Cypripedium acaule* and *Trillium undulatum*. For species with patchy distributions either additional shorter transects were used (*Aralia nudicaulis*, *Linnaea borealis*, *Medeola virginiana*, *Oxalis montana*) or all individuals found in the plots were sampled (*Chimaphila umbellata*, *Pyrola secunda*). Because phenological records for species occurring at both sites were very similar, the data are pooled in all presentations in this paper.

Flowering phenology

Before flowering commenced, sticky labels were attached to the stems of inflorescences and each was numbered. An average of approximately 200 flowering stems per species (range 64–797) were censused every 2nd day throughout the flowering period in 1979. In 1980, transect areas were halved and a smaller number of inflorescences were censused. Not all of the 12 species studied were surveyed in both years. *Trientalis borealis* was omitted in 1979, *Chimaphila umbellata* in 1980, and only incomplete data are available for *Cypripedium acaule* in 1980. On each census day the number of buds and open flowers per stem for each species was recorded. In species with a large number of flowers per inflorescence (*Aralia nudicaulis*, *Cornus canadensis*, *Maianthemum canadense*) the proportion of open flowers was estimated. Flowers were considered in anthesis when the stigma protruded from the corolla lobes or when the petals were open. End of flowering was identified by withering of the reproductive organs and discolouration of the petals. Data from the censuses were used to construct flowering curves (percentage of total flowers in anthesis, cumulative percentage of flowers in anthesis).

Fruiting phenology

Stems marked for flowering censuses were used to obtain data on fruiting phenology in 1979. The criteria for recognizing mature fruit depended on fruit type and species. For species with fleshy fruits (sarcophores), fruits were considered ripe when they had achieved a uniform colour (*Aralia nudicaulis* blue–black, *Clintonia borealis* blue, *Cornus canadensis* red, *Maianthemum canadense* red, *Medeola virginiana* blue–black, *Trillium undulatum* red). Rotting and withering of fruits were recorded as well as disappearance from the infructescence. Censuses were made at 2-day intervals until the end of September.

In species with dehiscent fruits (*Chimaphila umbellata*, *Cypripedium acaule*, *Pyrola secunda*) or explosive fruits (*Oxalis montana*) the criterion for maturity was dehiscence and loss of seeds from fruits.

The fruits of *Linnaea borealis* are desmochores and are bright green and gold at maturity, owing to the presence of sticky glandular hairs. The fate of these fruits after maturity was not followed because less than 5% disappeared from infructescences and the rest slowly withered in imperceptible stages during the subsequent period. Additional plants of *Cypripedium acaule* were located and surveyed because none of the individuals in the transects produced fruits.

To determine the extent of frugivory by animals of the six fleshy fruited species, comparisons of the rate of disappearance of fruit (due to either removal or disturbance causing falling) from protected and unprotected infructescences were made in 1979. The difference between the two treatments provides an estimate of the rate of fruit removal. Protected infructescences (ranging from 12 for *Aralia nudicaulis* to 41 for *Maianthemum canadense*) were enclosed by nylon mesh bags. Observations of the two treatments were made until the end of September, except for *Aralia nudicaulis* in which entire infructescences of both protected and unprotected treatments were entirely consumed by animals (probably deer) early in the fruiting season. Losses of fruit from protected and unprotected infructescences were compared using Kolmogorov–Smirnov two-sample tests (Siegel 1956).

Results

Flowering phenology

Figure 1 illustrates the patterns of flowering for the 12 boreal forest herbs at our study sites in central New Brunswick in 1979 and 1980. The flowering periods are distributed from mid-May to the end of July, although most species are in flower for less than a month. Sarcophorous species tend to flower early in the season. The peaks of most of the flowering curves illustrated in Fig. 1 are close to 100%, indicating a high degree of synchrony among inflorescences in flowering. This can be attributed to a combination of synchrony of anthesis of individual flowers and the duration of time that they remain open. The peaks range from 35 to 100% and are not easily divided into groups based on shape or height. Moreover, no trends are apparent in the curves with respect to time of flowering, although the two species with the lowest peaks flower late in the season. Some of the flowering curves are positively skewed, but this does not appear to be a general feature of the species in the community.

The climatic conditions differed considerably over the two years of the study (Fig. 2). In 1979 the mean temperature was several degrees higher in each of the months during which flowering occurred compared with 1980 (mean temperature (°C) 1979: May 12.4, June 16.9, July 20.0; 1980: May 9.9, June 14.8, July 18.3). Moreover, there was over twice as much precipitation in April and May of 1979 than in 1980, but June, the month in which most flowering occurs, was warm and dry in 1979 and cool and wet in 1980 (Fig. 2). These differences are associated with variation in the commencement of flowering of boreal forest herbs in the two years.

All species flowered later in 1980 than in 1979, although the order of flowering was maintained. In both years *Trillium undulatum* was first to reach peak flowering followed, approximately 3 weeks later, by *Maianthemum canadense*, *Clintonia borealis*, and *Aralia nudicaulis*. Next to flower were *Cornus canadensis* and *Cypripedium acaule*, followed serially by *Oxalis montana*, *Medeola virginiana*, *Linnaea borealis*, *Pyrola secunda*, and *Chimaphila umbellata*. Although the order of flowering was maintained in the two years, the delay of flowering in 1980 was not constant across species; however, no pattern is evident for a delay in either commencement or termination of flowering (Table 1).

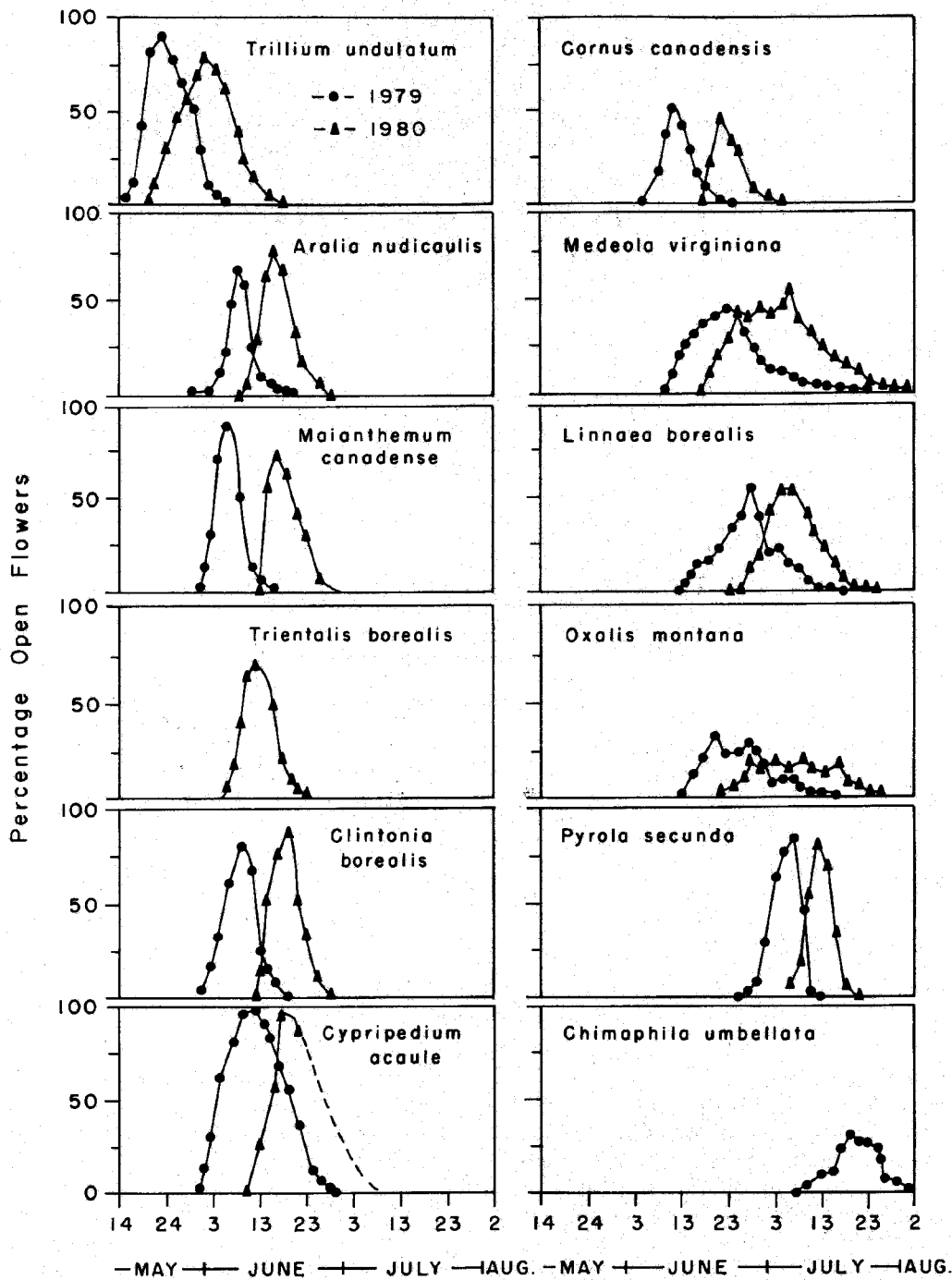


FIG. 1. Flowering phenology of boreal forest herbs at Doaktown, central New Brunswick, in 1979 and 1980. Curves are the percentage of total flowers censused in anthesis at intervals during the blooming period.

With the exception of *Trillium undulatum*, the species that flowered by mid-June (*Aralia nudicaulis*, *Maianthemum canadense*, *Clintonia borealis*, *Cornus canadensis*) had considerably shorter flowering periods in 1980. This resulted from a greater synchrony in the commencement of flowering of inflorescences (Table 1). *Trillium undulatum* differed in taking a longer rather than a shorter time to complete flowering. Duration of flowering for the species flowering after mid-June was almost identical in the two years. Data on the time from beginning of flowering to peak flowering in general show a similar pattern (Table 1). Thus, all species flowering before mid-June displayed differences in the synchrony of flowering

between years, whereas none of the later flowering species showed this effect.

Fruiting phenology

Cumulative flowering and fruiting curves for 1979 are illustrated in Fig. 3. Fruit maturation in the community began in mid-July and continued past the end of September. The order of fruiting does not correspond to the order of flowering. Furthermore, there is no association between fruiting time and fruit type. The six sarcochorous species mature fruit throughout the fruiting period, and of the four species with dehiscent fruit, one ripens fruit in late July, two in mid-September, and

TABLE 1. Comparison of flowering times of boreal forest herbs from central New Brunswick in 1979 and 1980

	No. of inflorescences sampled		Inflorescence life (days), \bar{X} (SD)		Duration of flowering (days)		No. of days from first open flower to peak flowering		Delay of flowering in 1980 relative to 1979 (in days) for:	
	1979	1980	1979	1980	1979	1980	1979	1980	first open flower	last open flower
<i>Trillium undulatum</i>	797	356	10.0(1.9)	10.6(2.1)	25	32	8	12	5	12
<i>Trientalis borealis</i>	—	182	—	6.8(2.4)	—	20	—	8	—	—
<i>Aralia nudicaulis</i>	168	292	12.2(3.0)	12.1(2.1)	28	20	12	10	11	3
<i>Maianthemum canadense</i>	210	100	8.4(1.9)	8.2(1.9)	22	14	8	4	13	5
<i>Clintonia borealis</i>	230	98	9.5(1.8)	9.4(1.7)	20	14	8	6	13	7
<i>Cypripedium acaule</i>	64	27	14.0(3.4)	—	30	—	11	4	13	—
<i>Cornus canadensis</i>	207	99	10.1(2.6)	8.6(2.8)	26	18	8	2	16	8
<i>Medeola virginiana</i>	115	85	21.9(8.6)	27.0(6.5)	45	48	15	16	11	14
<i>Linnaea borealis</i>	398	217	6.9(3.0)	7.4(2.5)	34	34	14	13	7	7
<i>Oxalis montana</i>	154	326	4.7(1.9)	5.0(1.8)	30	34	10	14	5	9
<i>Pyrola secunda</i>	142	75	10.2(2.7)	9.4(2.2)	20	18	10	6	10	8
<i>Chimaphila umbellata</i>	166	—	9.2(3.2)	—	30	—	8	—	—	—

TABLE 2. Comparison of flowering and fruiting periods of boreal forest herbs from central New Brunswick in 1979

	No. of days within which 95% of:		No. of days between first open flowers and first mature fruits
	flowers opened	fruits matured	
<i>Aralia nudicaulis</i>	14	32	42
<i>Chimaphila umbellata</i>	18	>12	71
<i>Clintonia borealis</i>	14	22	49
<i>Cornus canadensis</i>	16	26	46
<i>Cypripedium acaule</i>	12	12	111
<i>Linnaea borealis</i>	22	16	36
<i>Maianthemum canadense</i>	12	30	81
<i>Medeola virginiana</i>	30	28	76
<i>Oxalis montana</i>	22	12	34
<i>Pyrola secunda</i>	14	>18	79
<i>Trillium undulatum</i>	14	16	83

one in late September and beyond.

The interval between the beginning of flowering and the time when the first fruits have ripened ranges from 34 to 111 days (Table 2). Two major groups are evident with five species taking 34–49 days and five taking 71–83 days. Both groups contain some species with fleshy fruits and some with dehiscent fruits. The synchrony of flowering versus fruiting varies considerably among species (Table 2). The fruiting period was longer than the flowering period in five species, approximately equal in three, and shorter in two. Among species with fleshy fruits, fruiting periods were longer in four species and approximately equal in two.

The patterns of flowering and fruiting in *Oxalis montana* are of interest since the duration of flowering was about twice as long as that over which fruits dehisced (Fig. 3, Table 2). This would occur if the fruits that matured resulted from fertilization of flowers during a short time interval within the blooming period. However, this does not appear to be the case. Figure 4 compares the flowering pattern of all flowers with that of only those flowers that set fruit. The two curves are almost identical, indicating that significant heterogeneity exists in maturation rates of fruits produced at different times during the season. The time from flowering to fruit dehiscence is strongly negatively correlated with date of flowering (Fig. 5; $r =$

-0.88 , $P < 0.001$ using the Spearman rank correlation coefficient, $n = 35$). Fruits produced early in the blooming period took significantly longer to mature than did those that were initiated later in the season.

Fruit removal

Fruits of all six sarcochorous species were removed from infructescences by herbivores. No animals were observed feeding on fruits, but observations of partially eaten fruits as well as signs of disturbance of nearby vegetation suggest that the main herbivores were deer, small mammals, and birds. Figure 6 illustrates the percentage of fruits that fell or were removed from protected and unprotected infructescences. In each species the proportion of fruits removed or falling from unprotected infructescences was significantly greater than the proportion of fruits falling from protected infructescences (Table 3), indicating significant rates of fruit removal. Fruits of *Trillium undulatum* and *Aralia nudicaulis* were removed from infructescences more rapidly than those of other species. The removal of fruits from unprotected infructescences was similar for one pair of simultaneously fruiting species (*Maianthemum canadense*, *Medeola virginiana*) but not for another (*Clintonia borealis*, *Cornus canadensis*). With the exception of *Aralia nudicaulis*, the greatest rates of fruit removal (the

TABLE 3. Comparison of removal of fruit from protected and unprotected infructescences of six sarcochorous boreal forest herbs from central New Brunswick using Kolmogorov-Smirnov two-sample (one-tailed) tests

	Date of greatest difference	% fruit removed on date of greatest difference (n)		D	χ^2	P
		Unprotected	Protected			
<i>Aralia nudicaulis</i>	7 August	86.2 (1714)	5.7 (264)	0.805	592.98	<0.001
<i>Clintonia borealis</i>	11 September	70.7 (413)	6.5 (92)	0.642	124.04	<0.001
<i>Cornus canadensis</i>	29 September	46.1 (566)	8.2 (183)	0.379	79.46	<0.001
<i>Maianthemum canadense</i>	29 September	45.9 (246)	0.0 (178)	0.459	87.03	<0.001
<i>Medeola virginiana</i>	30 September	35.1 (74)	0.0 (18)	0.351	7.13	<0.05
<i>Trillium undulatum</i>	3 September	79.3 (305)	20.0 (15)	0.593	20.11	<0.001

TABLE 4. Fruit production as a function of flowering time of inflorescences in eight boreal forest herbs from central New Brunswick

	% fruit-set for inflorescences flowering at different times in the flowering period (no. of flowers)					χ^2	P
	Initial	Early	Peak	Late	Terminal		
<i>Chimaphila umbellata</i>	19.0 (58)	54.8 (177)	50.2 (203)	60.5 (172)	43.5 (23)	31.6	<0.001
<i>Clintonia borealis</i>	75.2 (109)	69.2 (214)	74.9 (167)	69.7 (221)	85.7 (42)	6.6	NS
<i>Cornus canadensis</i>	19.7 (529)	19.9 (1890)	8.9 (1638)	1.6 (630)	0 (101)	209.8	<0.001
<i>Linnaea borealis</i>	52.1 (48)	53.8 (52)	73.5 (162)	70.2 (84)	55.8 (52)	14.6	<0.01
<i>Maianthemum canadense</i>	14.4 (487)	12.4 (1563)	12.3 (1299)	7.8 (386)	3.7 (81)	14.8	<0.01
<i>Medeola virginiana</i>	8.1 (37)	23.7 (59)	10.3 (29)	20.8 (48)	44.7 (94)	26.8	<0.001
<i>Oxalis montana</i>	40.0 (30)	25.8 (31)	43.5 (46)	63.6 (11)	46.2 (13)	5.6	NS
<i>Pyrola secunda</i>	15.1 (53)	9.1 (231)	55.9 (535)	41.2 (136)	35.9 (39)	162.2	<0.001

steepest slopes in the curves of Fig. 6) occurred only after most of the fruit was ripe (see Fig. 3). In *Aralia nudicaulis*, fruit was removed rapidly after only 25% had ripened.

Differential fruit production during the flowering period

The relationship of the amount of fruit produced to time of flowering was examined for inflorescences of eight boreal forest herbs (Table 4). Inflorescences of each of these species were divided into five categories (equal in time) according to their time and duration of flowering. Because inflorescences in most species are in anthesis for a considerable portion of the total flowering period, they cannot be divided absolutely. The criterion used to assign inflorescences to categories was the midpoint of their time of flowering. Consequently, fertilization occurring on any specific day contributed to the fruit production of inflorescences in several categories. Not all inflorescences were assigned to the initial, early, peak, late, or terminal flowering categories to avoid ambiguous assignment. The criterion for fruit production was fruit development rather than production of mature fruit so that confounding with fruit predation and resource limitation would not occur.

Of the eight species tested, only *Clintonia borealis* and *Oxalis montana* showed no relationship between fruit production and time of flowering (Table 4). The other six species showed significant differences in fruit production among inflorescences in different phenological categories. The pattern of fruit production according to time of flowering differed. *Chimaphila umbellata* and *Medeola virginiana* had low fruit-set at the beginning of the flowering period. *Linnaea borealis* and *Pyrola secunda* had high fruit-set during peak flowering, and *Cornus canadensis* and *Maianthemum canadense* had low fruit-set at the end of flowering. There is a tendency for fruit production to vary with the number of inflorescences in bloom

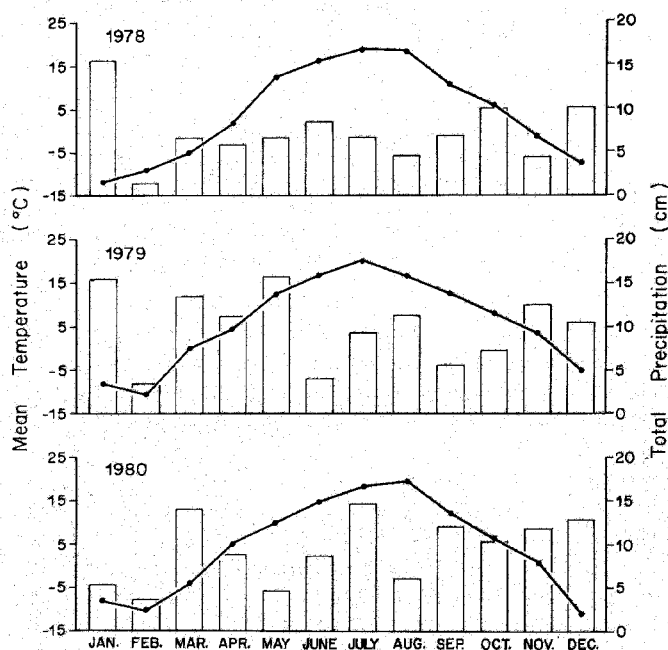


FIG. 2. Total monthly precipitation (cm) and mean monthly temperature ($^{\circ}\text{C}$) at Doaktown, central New Brunswick, for 1978–1980. Data obtained from Atmospheric Environmental Service, Environment Canada meteorological station at Doaktown.

at a given time; percent fruit production tends to be lower when there are fewer inflorescences in bloom. Spearman rank correlation coefficients calculated for percent fruit production and number of inflorescences in each category yielded significant values for *Linnaea borealis* and *Medeola virginiana* ($r =$

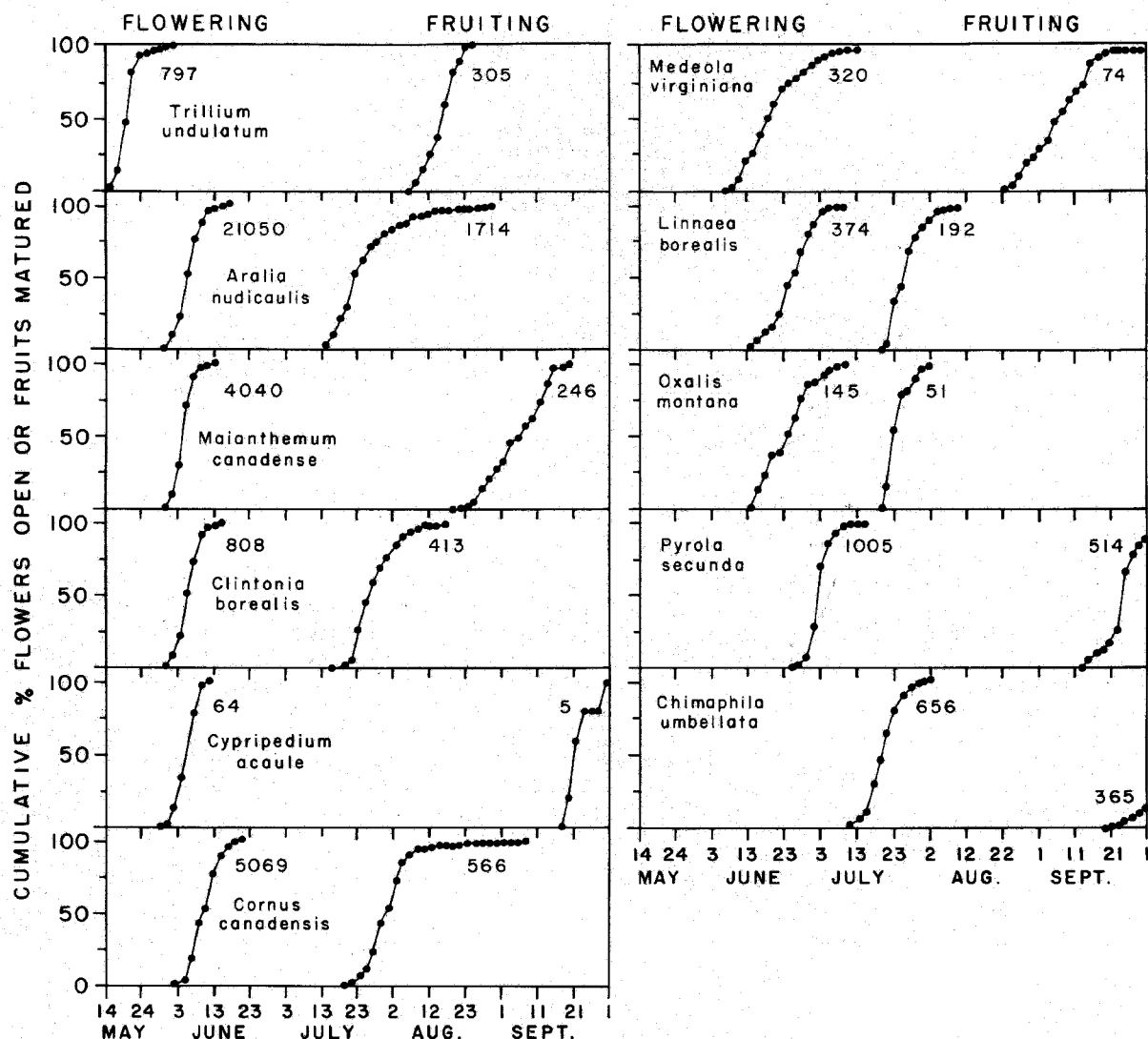


FIG. 3. Cumulative flowering and fruiting curves of boreal forest herbs at Doaktown, central New Brunswick, during 1979. Sample sizes for flowers and fruits censused are given for each species.

0.97 and $r = 0.90$, respectively; $P < 0.05$). Values for *Cornus canadensis* and *Maianthemum canadense* were also high ($r = 0.70$ for both species) but were not statistically significant because of the small number of categories used.

Fate of buds and fruits

The reproductive success of buds in producing mature fruit is affected at several stages (Table 5). Buds may never open and are aborted (*Chimaphila umbellata*, *Cornus canadensis*, *Pyrola secunda*), flowers may be eaten (*Pyrola secunda*, *Trillium undulatum*) or wither prematurely (*Chimaphila umbellata*), fruit development may fail to occur (all species, but especially the self-incompatible *Cornus canadensis*, *Maianthemum canadense*, and *Medeola virginiana*), and developing fruit may either abort (*Cornus canadensis*, *Maianthemum canadense*) or be removed from infructescences (*Aralia nudicaulis*, *Clintonia borealis*). These data allow us to compare the "efficiency" of sexual reproduction in boreal forest herbs. The number of mature fruits, expressed as a percentage of flower buds produced, ranges from 0 to 61%. Discounting the dioecious *Aralia nudicaulis*, in which male buds were not included in the calculations, and *Cypripedium acaule*, in

which no fertilizations occurred in our sample, the range extends from 6 to 50%. Successful fruit production does not appear to be correlated with fruit type or time of flowering, although sarcochorous fruits are more likely to be removed by animals while still unripe. Breeding system is, however, partly associated with fruiting success (with the exception of *Cypripedium acaule*, which received little pollinator service; see Barrett and Helenurm 1987), with the lowest fruit production experienced by self-incompatible species (*Cornus canadensis*, *Maianthemum canadense*, *Medeola virginiana*). Data are not available for *Trientalis borealis*, the only other self-incompatible species examined. Dioecious *Aralia nudicaulis* experienced the highest fruiting success of the species examined.

The fate of sarcochorous fruits is shown in Table 6. One-third of the fruit of *Cornus canadensis* and a small proportion of fruit in three other species rotted. A small proportion of fruit from all six species dried or withered on infructescences. A large proportion of fruit disappeared from infructescences. This is probably due mainly to removal by herbivores, although in *Trillium undulatum* many fruits were found unharmed on the ground immediately below the plant and the

TABLE 5. Reproductive success of buds in developing mature fruit in boreal forest herbs from central New Brunswick

	No. of plants sampled	No. of buds produced	% opening	% surviving flowering period	% developing fruit	% maturing fruit
<i>Aralia nudicaulis</i> ^a	232	17446	—	—	68.9	60.6
<i>Chimaphila umbellata</i>	166	800	83.1	76.5	46.9	45.6
<i>Clintonia borealis</i>	230	833	99.0	97.0	69.3	49.6
<i>Cornus canadensis</i>	207	5221	86.8	84.8	13.1	10.8
<i>Cypripedium acaule</i>	64	64	100.0	95.3	0.0	0.0
<i>Linnaea borealis</i>	398	534	94.9	93.6	48.7	48.7
<i>Maianthemum canadense</i>	210	4263	95.0	92.8	11.6	5.8
<i>Medeola virginiana</i>	115	338	97.0	89.9	21.9	21.9
<i>Oxalis montana</i>	154	154	98.0	97.4	34.4	34.4
<i>Pyrola secunda</i>	142	1479	81.6	68.0	34.8	34.8
<i>Trientalis borealis</i>	188	240	92.5	92.5	—	—
<i>Trillium undulatum</i>	797	797	100.0	91.5	38.3	38.3

^aAdditional data were used from the 1-ha block described in Barrett and Helenurm (1981).

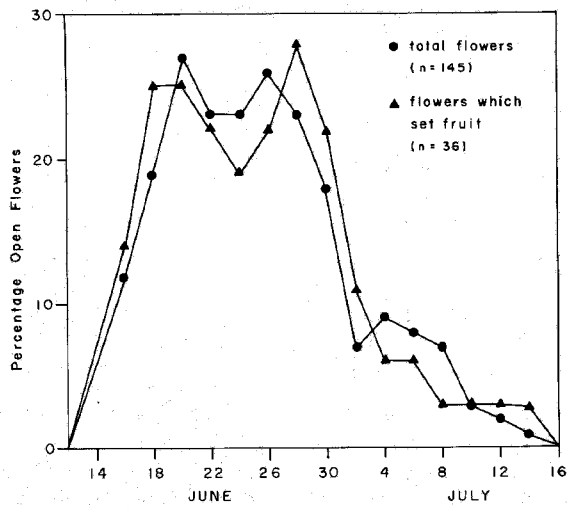


FIG. 4. Flowering phenology of all *Oxalis montana* ramets that were censused in 1979 and those that set fruit.

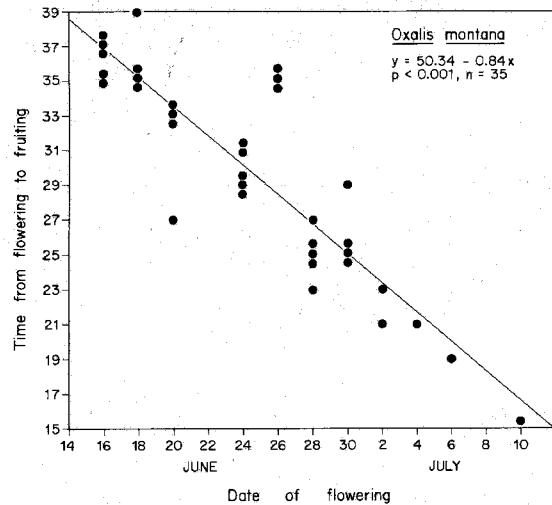


FIG. 5. The relationship between the date of flowering and the time taken from flowering to capsule dehiscence in *Oxalis montana* in 1979.

species has ant-dispersed seeds. Seed predation occurred in a quarter of the fruits produced by *Clintonia borealis*, with empty fruits found within a metre of marked plants. Finally, it should be noted that the proportion of fruits remaining on infructescences was partly an artifact of the time in the fruiting period during which sampling was discontinued. Apart from *Aralia nudicaulis* the remaining five species dispersed between 30 and 66% of their seeds by the end of September 1979. Fruits of *Cornus canadensis*, *Maianthemum canadense*, and *Medeola virginiana* were still being removed at that time.

Discussion

The community of understory herbs at our study sites in central New Brunswick is composed of relatively few angiosperm species. The 12 species examined jointly account for over 95% of the herbaceous cover (Barrett and Helenurm 1987). Although this feature considerably simplifies the logistics of community research, it may at the same time increase the difficulty of interpretation of data. Patterns at the community level may be less easily detected owing to the small number of species. Analogous to the way in which sampling error has a greater impact on small samples drawn from a population, it is more likely that a small group of species appears as a random

assemblage than a large group, regardless of whether patterns actually exist.

The flowering and fruiting times of boreal forest herbs may have been selected within rather broad limits imposed largely by abiotic features of the environment and their influence on the physiology and development of flower and fruit maturation. In addition, phylogenetic and life-history constraints influence the evolution of reproductive patterns (Kochmer and Handel 1986) and may in part determine the seasonal limitations to flowering periods in boreal forest herbs. Nevertheless, biotic interactions are obviously important for sexual reproduction since all the species we studied are insect pollinated and half bear fleshy, animal-dispersed fruits. However, the biotic interactions appear to be generalized and unspecific in nature. Flowers of all of the species we examined are visited by many species of generalized pollinators (Barrett and Helenurm 1987), so that as long as flowering occurs during periods of insect activity, the precise timing of flowering may be of relatively little consequence. Similarly, during the fruiting period a variety of animals appear to account for fruit removal in the sarcochorous species. As long as fruit production occurs while at least some of these animals are foraging, the production of

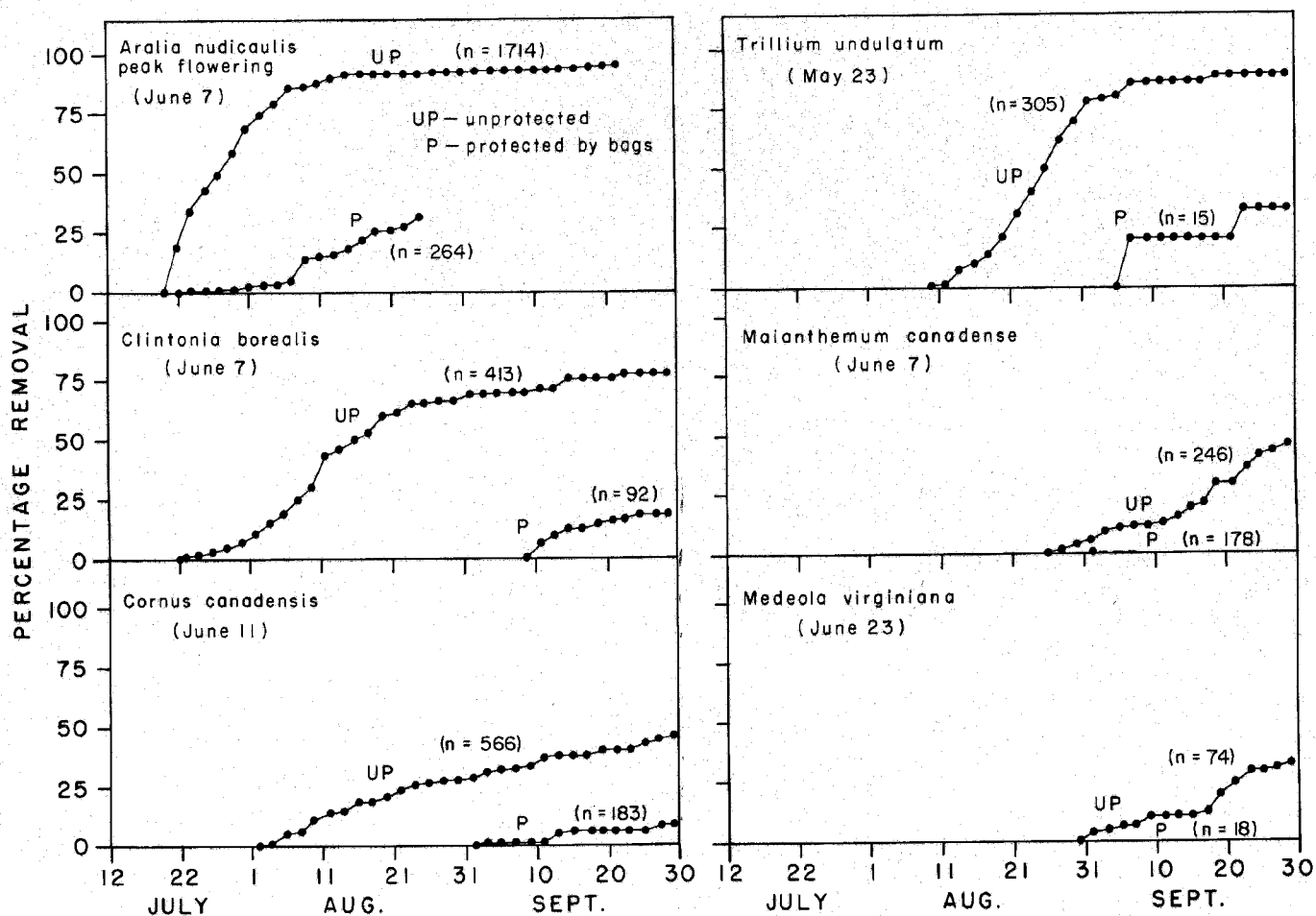


FIG. 6. Comparison of the percentage of fruits that were removed or fell from protected and unprotected infructescences of six sarcochorous boreal forest herbs from central New Brunswick in 1979.

TABLE 6. Fate of fruits produced from maturation until the end of September by six sarcochorous boreal forest herbs from central New Brunswick

	No. of infructescences sampled	Total no. of fruits produced	% rotted	% withered	% on ground below plant	% in which seeds removed	% disappeared	% remaining
<i>Aralia nudicaulis</i>	40	1714	0.0	4.4	0.0	0.0	95.4	0.2
<i>Clintonia borealis</i>	159	413	6.8	6.8	1.2	23.7	51.3	10.2
<i>Cornus canadensis</i>	81	566	33.2	3.7	5.1	0.2	40.8	17.0
<i>Maianthemum canadense</i>	73	246	4.9	7.7	4.9	0.0	41.1	41.4
<i>Medeola virginiana</i>	34	74	0.0	6.8	0.0	0.0	31.1	62.1
<i>Trillium undulatum</i>	305	305	7.2	3.3	22.0	0.3	66.2	1.0

mature fruit at a specific time during the season may have little significance.

The limit to how early flowering can begin is probably set by temperature conditions. Some growth must occur in all species before inflorescences commence anthesis, so flowering must be delayed until suitable conditions for growth have existed for a few weeks. Moreover, temperatures must be high enough to ensure some insect visitation after flowers have opened. Bumblebees, which are major pollinators in this community and which fly at lower temperatures than most pollinators, generally restrict foraging to ambient temperatures above 10°C (Heinrich 1979). Mean maximum temperatures in central New Brunswick do not reach 10°C until May, and maximum temperatures rarely exceed 10°C in April (from Environment Canada meteorological station reports for Doaktown). Frosts

occur as late as June. Flowering in the community, therefore, may occur as early as temperatures permit, with most species flowering by the end of June. Interestingly, the species that flowers earliest, *Trillium undulatum*, appears to be apomictic and may not be dependent upon insect visitation for seed set (Barrett and Helenurm 1987).

The limit to how late fruiting can occur may also be set by temperature. Frosts can begin as early as mid-August and are frequent in September. Most of the species matured fruit before mid-September. Selection on flowering and fruiting times may, of course, be influenced by other ecophysiological adaptations. Specifically, flowering times may be constrained by selection on fruiting times and vice versa (Primack 1985; Rathcke and Lacey 1985). A minimum period necessary for fruit development exists in all species, so that flowering must

occur sufficiently early to permit fruit maturation before the onset of cold weather. The limit to how early fruit can ripen is partly set by the time required for flowering and fruit maturation to occur.

Phenological studies of other temperate communities have indicated the importance of abiotic factors to phenological patterns as well. Many of these studies also failed to reveal obvious patterns or associations of species within the broad limitations imposed by the environment. Schemske *et al.* (1978) found that flowering in seven spring woodland herbs of central Illinois generally began as soon as temperatures were suitable for plant growth and pollinator activity, and ended before canopy closure. Beyond this, the flowering times were not finely tuned to temperature regime or pollinator activity. In the Chilean Andes, flowering extends from the date of snowmelt to late summer and early autumn (Arroyo *et al.* 1981). Peak flowering coincided with maximum temperatures at some, but not all, altitudes. Mosquin (1971) found that flowering began after snowmelt in subalpine vegetation in the Bow River Valley in western Canada and in North American tall-grass prairie, the temporal dispersion of flowering times for different species was indistinguishable from a random collection (Rabinowitz *et al.* 1981).

There are several examples in our data of the effect of local climate on the timing of reproductive events. In the 1979 season, for example, *Aralia nudicaulis*, *Clintonia borealis*, and *Maianthemum canadense* all achieved peak flowering on June 8, the first warm and sunny day in over a week. The simultaneous dip in the flowering curves of *Medeola virginiana*, *Linnaea borealis*, and *Oxalis montana* in early July coincided with the first two rainy and cool days in over a week. The comparison of flowering times for 1979 and 1980 is particularly interesting: flowering order was maintained, but the species were affected differently in delay of anthesis, synchrony, and duration of flowering. Flowering occurred later in 1980 than in 1979 for most of the early-flowering species because of an extended winter, but it was more highly synchronized so that the end of the flowering period was delayed much less than the beginning. Risser and Cottam (1967) found a similar response in the vegetative growth of several spring ephemerals. Increased lengths of cold treatment decreased the time required for subsequent emergence and growth. Although we have no information on the vegetative growth of boreal forest species, it is possible that the same mechanism caused the delayed but more highly synchronized flowering in 1980.

Similar effects of local climate on the timing of reproductive events may occur during the fruiting period. The explosive fruits of *Oxalis montana* all dehisced within 12 days, although they were produced from flowers that opened during the whole range of the 22-day flowering period in the species. Several days of very warm and sunny weather preceded this sudden burst of dehiscence. Most of the dehiscent fruits of *Cypripedium acaule* and *Pyrola secunda* split within the same 8-day period in September, although their flowering periods were separated by about 1 month. Again, several days of warmer, sunny weather occurred at the start of the period of dehiscence. Local climate may influence the success of a seed crop in this manner. The time of parturition relative to time of germination is a potentially important factor in the life cycle because of the risk of seed mortality in the soil (Schaal and Leverich 1981).

Several factors appear to limit fruit production in boreal forest herbs. Developing fruit were lost through predation in *Aralia nudicaulis* and *Clintonia borealis* and pollen limitation

is suggested in *Cornus canadensis*, *Cypripedium acaule*, *Medeola virginiana*, *Oxalis montana*, and *Trientalis borealis* by the elevated fruit-set observed as a result of hand-pollinations in comparison with open-pollinated flowers (Barrett and Helenurm 1987). This may occur because of extended periods of inclement weather or possibly because of a shortage of pollinators due to the extensive overlaps in flowering time of most of the species. However, in the absence of more detailed data, it is not possible to comment on hypotheses regarding competition among species for pollinators. Breeding system, however, appears to play an important role in determining levels of fruit production in boreal forest herbs with self-incompatibility strongly associated with low fruit-set. This may occur because of low levels of effective pollination despite frequent pollinator visits. Because of the extensive clonal growth of several of these species and their consequent patchy distribution, it is possible that many pollinator visits result in the deposition of incompatible pollen on stigmas. Effective compatible pollinations may occur only as often as interpatch pollinator flights. Data regarding pollinator flight patterns and population structure of the plant species are needed to test this hypothesis.

Low light levels and nutrient-poor soils are likely to restrict the reproductive capacity of most, if not all, of the herbs we studied by placing restrictions on flowering and fruiting. Although fruit abortion was observed in only two species (*Maianthemum canadense*, 50.1% of developing fruits, and *Cornus canadensis* 17.5%), suggesting some resource limitation of fruit-set, more detailed studies are required to evaluate the role of resource limitation in regulating the fruit-set and seed set of individuals. In particular, it will be of importance to assess the effects of the interaction between mating type (self, sibling, or outcrossed mating) and resource levels on fruit and seed abortion, seed production, and seed weight. Recent studies by Galen *et al.* (1985) and Galen and Weger (1986) have begun to explore the complex interactions between these factors in *Clintonia borealis*.

Tests for differences in the levels of fruit-set of inflorescences in anthesis at different times during the flowering period yielded a variety of patterns. Depressed fruit-set occurred early during flowering in two species (*Chimaphila umbellata* and *Medeola virginiana*) and late during flowering in another two (*Cornus canadensis* and *Maianthemum canadense*). Two species produced more fruit during peak flowering than during either early or late flowering (*Linnaea borealis* and *Pyrola secunda*), while the last two species examined were apparently unaffected by time of flowering (*Clintonia borealis* and *Oxalis montana*). Variation in fruiting levels appears to be mainly associated with the number of inflorescences in anthesis at a given time, suggesting that pollinators may respond to high densities of inflorescences with increased visitation.

Removal of fruit from infructescences of sarcochorous species coincided with peak fruiting in 5 of the 6 species. Only in *Aralia nudicaulis* did fruit removal occur consistently throughout the period of fruit maturation. This suggests a density-dependent relationship in fruit removal for most species, with removal rates increasing as a result of an increasing density of mature fruit for consumption. It is also possible, however, that fruiting time has been selected to coincide with the availability of fruit dispersers. It is not possible to distinguish between these ideas with correlational data alone. Indirect evidence bearing on this issue includes the distribution

of fruit maturation times of different species over much of the season, the apparent absence of large influxes of animals at any time within the fruiting season, and the constraints on time of fruit production imposed by the short growing season. These lines of evidence suggest that fruit removal may result primarily from opportunistic behaviour of the local fauna when fruits are available.

The sarcochorous species fruit at different times and are not amenable to grouping according to either the shape of the fruit maturation curve or time. These results contrast with those of Thompson and Willson (1979), who found that most sarcochores matured fruit synchronously among plants during the period of fall bird migration and that these species experienced the highest removal rates. They also reported that earlier fruiting species matured fruits asynchronously and had lower removal rates. With boreal forest species, the earliest fruiting species did so asynchronously, yet experienced high removal rates throughout the fruiting period. Although some species ripened fruit during the period of fall migration, there was no overall tendency for sarcochores to do so. Detailed information is not available, but bird migration appears to occur at a relatively consistent rate from mid-August through mid-November (Eastwood 1967). Birds may be less important as dispersal agents in this community or the constraints of development time and an early winter may preclude precise timing of fruit maturation to peak frugivore availability.

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- ARROYO, M. T. K., ARMESTO, J. J., and VILLAGRAN, C. 1981. Plant phenological patterns in the high Andean cordillera of central Chile. *J. Ecol.* **69**: 205–223.
- BARRETT, S. C. H., and HELENURM, K. 1981. Floral sex ratios and life history in *Aralia nudicaulis* (Araliaceae). *Evolution* (Lawrence, Kans.), **35**: 752–762.
- . 1987. The reproductive biology of boreal forest herbs. I. Breeding systems and pollination. *Can. J. Bot.* This issue.
- CROAT, T. B. 1969. Seasonal flowering behavior in central Panama. *Ann. Mo. Bot. Gard.* **56**: 295–307.
- DAUBENMIRE, R. 1972. Phenology and other characteristics of tropical semi-deciduous forest in north-western Costa Rica. *J. Ecol.* **60**: 147–170.
- EASTWOOD, E. 1967. Radar ornithology. Methuen and Co., London.
- FRANKIE, G. W., BAKER, H. G., and OPLER, P. A. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *J. Ecol.* **62**: 881–919.

- 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.
- HEINRICH, B. 1976. Flowering phenologies: bog, woodland, and disturbed habitats. *Ecology*, **57**: 890–899.
- . 1979. Bumblebee economics. Harvard University Press, Cambridge.
- KOCHMER, J. P., and HANDEL, S. N. 1986. Constraints and competition in the evolution of flowering phenology. *Ecol. Monogr.* In press.
- MCCLURE, H. E. 1966. Flowering, fruiting and animals in the canopy of a tropical rain forest. *Malay For.* **29**: 182–203.
- MONASTERIO, M., and SARMIENTO, G. 1976. Phenological strategies of plant species in the tropical savannah and the semideciduous forest of the Venezuelan llanos. *J. Biogeogr.* **3**: 325–386.
- MOSQUIN, T. 1971. Competition for pollinators as a stimulus for the evolution of flowering time. *Oikos*, **22**: 398–402.
- OPLER, P. A., FRANKIE, G. W., and BAKER, H. G. 1976. Rainfall as a factor in the release, timing, and synchronization of anthesis by tropical trees and shrubs. *J. Biogeogr.* **3**: 231–236.
- POJAR, J. 1974. Reproductive dynamics of four plant communities of southwestern British Columbia. *Can. J. Bot.* **52**: 1819–1834.
- PRIMACK, R. B. 1985. Patterns of flowering phenology in communities, populations, individuals and single flowers. In *The population structure of vegetation*. Edited by J. White. Dr. W. Junk Publishers, Dordrecht. pp. 571–593.
- RABINOWITZ, D., RAPP, J. K., SORK, V. L., RATHCKE, B. J., REESE, G. A., and WEAVER, J. C. 1981. Phenological properties of wind- and insect-pollinated prairie plants. *Ecology*, **62**: 49–56.
- RATHCKE, B. J., and LACEY, E. P. 1985. Phenological patterns of terrestrial plants. *Annu. Rev. Ecol. Syst.* **16**: 179–214.
- RISSE, P., and COTTAM, G. 1967. Influence of temperature on the dormancy of some spring ephemerals. *Ecology*, **48**: 500–503.
- ROWE, J. S. 1972. Forest regions of Canada. Canadian Forest Service, Department of the Environment, Ottawa, Ont. Publ. 1300.
- SCHAAL, B. A., and LEVERICH, W. J. 1981. The demographic consequences of two-stage life cycles: survivorship and the time of reproduction. *Am. Nat.* **118**: 135–138.
- SCHEMSKE, D. W., WILLSON, M. F., MELAMPY, M. N., MILLER, L. J., VERNER, L., SCHEMSKE, K. M., and BEST, L. B. 1978. Flowering ecology of some spring woodland herbs. *Ecology*, **59**: 351–366.
- SIEGEL, S. 1956. Nonparametric statistics for the behavioural sciences. McGraw-Hill, New York.
- SNOW, D. W. 1965. A possible selective factor in the evolution of fruiting seasons in tropical forest. *Oikos*, **15**: 274–281.
- STILES, E. G. 1977. Coadapted competitors: the flowering seasons of hummingbird-pollinated plants in a tropical forest. *Science* (Washington, D.C.), **198**: 1177–1178.
- THOMPSON, J. N., and WILLSON, M. F. 1979. Evolution of temperate fruit/bird interactions: phenological strategies. *Evolution* (Lawrence, Kans.), **33**: 973–982.