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## SPATIAL AND TEMPORAL VARIATION IN CHASMOGAMY AND CLEISTOGAMY IN *OXALIS MONTANA* (OXALIDACEAE)<sup>1</sup>

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### ABSTRACT

Chasmogamous (CH) and cleistogamous (CL) flower production was investigated in natural populations of the perennial herb *Oxalis montana* in southern Quebec, Canada. Every 10-12 days during two flowering seasons, we recorded the reproductive output of approximately 2,000 plants distributed among five forest sites. The percentage of plants flowering, proportion of flowering plants producing CH and CL flowers, CH and CL flower number per flowering plant, and the proportion of flowers that are CL differed significantly among sites and corresponded to site differences in forest type and habitat quality. Unlike patterns in most CL species, however, reproduction by cleistogamy increased in sites with habitat conditions favorable to plant growth and sexual reproduction, and decreased in less productive sites. Chasmogamous and CL flower production increased with increasing plant size but plant size explained a significantly greater proportion of the variation in CL flower numbers. The percentage of flowering plants producing CH flowers decreased between years while the proportion of CL flowers increased at all sites during the second flowering season. The somewhat unusual aspects of reproduction in *Oxalis* may stem from its perennial habit which allows use of stored resources in adjusting the balance of cleistogamy versus chasmogamy in different environmental regimes.

THE PRODUCTION of distinct chasmogamous (CH) and cleistogamous (CL) flowers (Darwin, 1877; Lord, 1981; Campbell et al., 1983) represents a multiple strategy of reproduction with important implications for plant fitness (Lloyd, 1984; Schoen and Lloyd, 1984). Chasmogamous flowers provide a means of outcrossing and donation of pollen to other plants in the population, but risk pollination failure (Darwin, 1877; Schemske, 1978; Lord, 1981; Schoen and Lloyd, 1984). Cleistogamous flowers, in contrast, remain closed through their development and are structurally modified to ensure self-pollination (Lord, 1981). Moreover, they are often markedly reduced in size and cost of production (McNamara and Quinn, 1977;

Schemske, 1978; Waller, 1979; Wilken, 1982; Schoen, 1984; Jasieniuk, 1985). Reproduction by CL flowers provides greater resource economy and certainty of fertilization relative to reproduction by CH flowers, but can potentially result in progeny with reduced fitness due to inbreeding depression (Waller, 1984; Clay and Antonovics, 1985; Mitchell-Olds and Waller, 1985). In species with such mixed mating systems, adaptation to environments that are heterogeneous in space and time can be achieved by adjusting the relative allocation of resources to the alternative reproductive modes to correspond to the incidence of environments in which each mode is more successful (Lloyd, 1984). Consequently, natural populations of perennial species with mixed mating systems should exhibit both spatial and temporal variation in the relative production of CH and CL flowers that is related to environmental variation.

The purpose of this study was to examine variation in cleistogamy and chasmogamy in natural populations of wood sorrel, *Oxalis montana*, in different habitats over time. Since a large proportion of plants in all habitats remained vegetative through the flowering season and produced neither CH nor CL flowers, we first examined variation in the percentage of flowering plants among sites and years, and then investigated patterns of CH and CL flower production.

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**MATERIALS AND METHODS**—*Species studied*—*Oxalis montana* is common in rich, moist forests of eastern Canada and the northeastern United States (Fernald, 1950; Scoggan, 1978). It spreads clonally by slender rhizomes which root adventitiously to produce discrete patches of plants (ramets) with prominent fleshy petiole bases (Packham, 1978). In the populations we studied, a single patch of *Oxalis* contained up to 59 ramets with median patch sizes ranging from 4 to 11 ramets. Between 36 and 64% of the ramets in our populations were solitary, and only between 2 and 20% were connected to more than 3 other ramets. The level of physiological integration among ramets in patches of *Oxalis* is therefore likely to be low (Pitelka and Ashmun, 1985), and we have consequently analyzed our data as though each ramet is an independent plant.

Plants either remain vegetative throughout the flowering season, or reproduce by CH flowers, CL flowers, or both. All flowers are produced singly on peduncles arising from the petiole bases. Chasmogamous flowers are 5-merous and actinomorphic. Petals are white with purple veins serving as nectar guides and small patches of gold at the base marking the position of nectaries (Vereshchagina, 1965; Packham, 1978). Chasmogamous flowers are slightly protandrous with the 10 anthers releasing their pollen as the stigmas are exerted. Insect visitors include flies, thrips, beetles, and bees (Vereshchagina, 1965; Packham, 1978; Jasieniuk, unpublished). Cleistogamous flowers are greatly reduced in size and remain closed throughout their development. Anthers contain few pollen grains which germinate within the anther. Pollen tubes grow through the anther wall to the stigma (Vereshchagina, 1965; Packham, 1978; Jasieniuk, unpublished). The morphology and postfertilization development of the ovary is the same for both floral forms. The ovary consists of five fused carpels each containing one ovule and forming a loculicidal capsule at maturity. Capsules contain from 1–5 seeds that are dispersed ballistically up to a meter from the parent plant (Packham, 1978; Jasieniuk, unpublished).

*Sites*—Field investigations were conducted at five sites chosen to represent a diversity of habitat conditions in southern Quebec, Canada. Two sites were located at the University of Montreal field station near St. Hippolyte (45°59'N, 74°00'W). Three sites were located at the Lac Commandant Properties near Montebello (45°39'N, 74°56'W). The St. Hippolyte populations included 1) a wet, lake edge habitat of deeply shaded coniferous woods dominated

by *Abies balsamea* and few understory herbs (SH-LE); and 2) an upland deciduous forest stand dominated by *Acer rubrum* and supporting a luxuriant and diverse understory (SH-UF). The three Montebello sites included 1) a dry, sandy hilltop with a sparse ground cover under a canopy of predominantly *Tsuga canadensis* (M-HT); 2) a deeply shaded forest edge stand bordering a stream and dominated by *Thuja occidentalis* with few understory herbs (M-FE); and 3) a mesic upland deciduous forest dominated by *Acer saccharum* with a luxuriant and diverse herbaceous understory (M-UF).

*Sampling methods*—One hundred patches of *Oxalis montana* (approximately 90% of all plants in a population) were flagged at each site, and 40 were chosen randomly for further study. All plants in the selected patches were marked with colored thread, and their size and CH and CL flower production recorded.

Size was measured in terms of total leaf area per plant. We recorded the widths (in cm) of all leaves on a plant and subsequently converted these measures into leaf area (in cm<sup>2</sup>). The conversion equation was obtained by collecting an independent random sample of 400 leaves, covering the range of sizes possible, from plants growing outside the selected patches. The width of each leaf was measured and the corresponding area obtained using a Paton electronic planimeter. The least squares regression equation was used to calculate leaf area from leaf width for the marked plants:

$$\ln(\text{leaf area in cm}^2) = 1.986 \ln(\text{leaf width in cm}) + 4.018, r^2 = 0.98 \text{ and } P < 0.0001.$$

Chasmogamous and CL flower production were determined by recording the number and type of flowers on all marked plants every 10 to 12 days through the flowering seasons of 1980 and 1981. Since CL flowers require 28–49 days to mature from early bud state to capsule dispersal, while CH flowers require 33–61 days (Jasieniuk, 1985), the sampling interval ensured that all flowers produced by plants during a flowering season were scored.

Tests of independence using the *G* statistic (Sokal and Rohlf, 1981) were used to analyze frequencies. The linear regressions and analysis of covariance were done using Version 5 of SAS (SAS Institute, 1985).

**RESULTS**—*CH and CL flower production*—Chasmogamous and CL flower production in *Oxalis montana* varied temporally during a single flowering season (Fig. 1). Chasmogamous flowers were produced before CL flowers from mid-June to early or mid-July; CL flowers

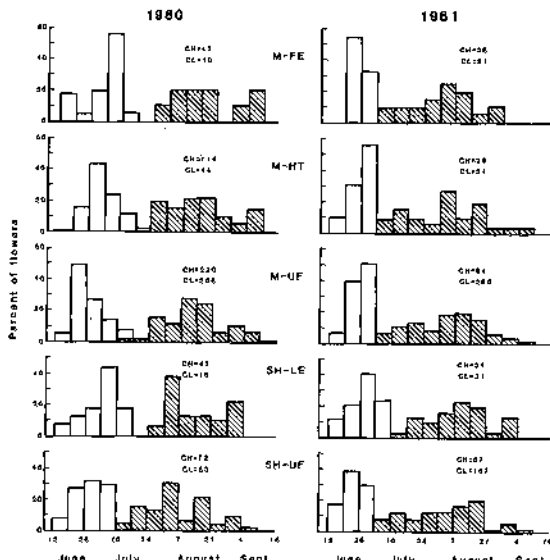


Fig. 1. Temporal variation in CH (open bars) and CL (hatched bars) flowering during a single flowering season. Numbers of flowers for each site and year are indicated.

were produced from early or mid-July to mid- or late September. There was almost no overlap in CH and CL flowering periods. The duration of flowering also differed for the two floral forms (Fig. 1). Chasmogamous flowering was completed in 3–5 wk while CL flowering continued for a period of approximately 7–10 wk.

The percentage of plants flowering (producing any CH or CL flowers) ranged from 10.8 to 54.8% among sites in 1980 and from 11.6 to 48.5% in 1981 (Table 1). Between-site differences in the frequency of flowering plants were highly significant (1980:  $G = 251.3$ ,  $df = 4$ ,  $P < 0.01$ ; 1981:  $G = 222.2$ ,  $df = 4$ ,  $P < 0.01$ ). During the two years of the study, percent flowering was lowest in the deeply shaded coniferous woods sites, M-FE and SH-LE, and highest in the sunnier, mostly deciduous, up-

land forest site, M-UF (Table 1). In contrast, between-year differences were not significant ( $G < 3.8$ ,  $df = 1$ ,  $P > 0.05$  for each site). All populations consisted of roughly the same proportion of flowering plants in 1981 as 1980 (Table 1).

The percentage of flowering plants producing CH flowers at each site in 1980 ranged from 73.7 to 86.8% (Table 1). Between-site differences were not significant ( $G = 7.9$ ,  $df = 4$ ,  $P > 0.05$ ). In contrast, the proportion of flowering plants producing CL flowers in the same year was considerably lower at most sites, ranging from 25.0 to 67.9%. Between-site differences were highly significant ( $G = 62.4$ ,  $df = 4$ ,  $P < 0.01$ ). Percent of flowering plants producing CL flowers was lowest in the deeply shaded coniferous woods sites, M-FE and SH-LE, and highest in the sunnier, mostly deciduous, upland forest sites, M-UF and SH-UF.

The percentage of flowering plants producing CH and CL flowers at each site in 1981 differed markedly from those of the previous year (Table 1). There was a significant decrease in the proportion of plants producing CH flowers ( $G = 64.8$ ,  $df = 4$ ,  $P < 0.01$ ), and a significant increase in the proportion of plants producing CL flowers ( $G = 64.3$ ,  $df = 4$ ,  $P < 0.01$ ). Percent of flowering plants producing CH flowers at each site ranged from 45.5 to 77.6% and differed significantly among the five populations ( $G = 24.6$ ,  $df = 4$ ,  $P < 0.01$ ) in contrast to the uniform proportions observed among sites during the 1980 flowering season. Between-site differences in the percentage of flowering plants producing CL flowers were also highly significant ( $G = 68.7$ ,  $df = 4$ ,  $P < 0.01$ ) ranging from 40.8 to 89.0%.

Chasmogamous and CL flower number per plant ranged from 1 to 5 although most plants produced only one or two during a flowering season (Fig. 2). Both CH and CL flower number per plant differed significantly among sites (CH flowers:  $G = 62.8$ ,  $df = 16$ ,  $P < 0.01$ ; CL

TABLE 1. Percent of plants flowering, and percent of flowering plants producing CH and CL flowers, at each site during two flowering seasons

	1980			1981		
	Flowering (N) <sup>a</sup>	CH	CL	Flowering (N) <sup>a</sup>	CH	CL
Montebello						
Forest edge	14.7 (326)	83.3	25.0	13.1 (375)	77.6	40.8
Hilltop	31.7 (348)	83.6	36.4	24.8 (230)	59.6	70.2
Upland forest	54.8 (409)	73.7	67.9	48.5 (507)	45.5	89.0
St. Hippolyte						
Lake edge	10.8 (490)	86.8	26.4	11.6 (517)	60.0	58.3
Upland forest	24.2 (413)	78.0	52.0	22.6 (550)	63.7	66.9

<sup>a</sup> Number of plants sampled.

flowers:  $G = 33.7$ ,  $df = 16$ ,  $P < 0.01$ ). To a large extent, site differences in flower production paralleled site differences in the percentage of plants flowering at a site. Sites M-UF, SH-UF, and M-HT not only had the highest proportion of flowering plants, flowering plants also produced a larger number of flowers per plant than those in the remaining sites (Table 1, Fig. 2). In contrast, the percentage of flowering plants was lowest, as was flower number per plant, in sites M-FE and SH-LE. Between-year differences in CH flower number per plant were not significant ( $G = 0.7$ ,  $df = 4$ ,  $P > 0.05$ ). In contrast, CL flower number per plant increased significantly in 1981 compared to 1980 ( $G = 10.8$ ,  $df = 4$ ,  $P < 0.01$ ).

In general, CH and CL flower production per plant increased with increasing plant size (total leaf area) (Fig. 3, Table 2). There were significant differences in the flower number-plant size relationships, however, among years, sites, and flower types (Table 3). Effects of interactions between the factors were also significant. In general, CL flower production was dependent on plant size to a greater degree than CH flower production (Table 2). This was particularly true in 1980 when CH flower number per plant was independent of plant size in three of the five sites ( $P > 0.05$ ) and only slightly dependent ( $P < 0.05$ ,  $r^2 < 0.05$ ) in the remaining sites. Plant size explained a significantly greater proportion of the variation in CL relative to CH flower production at all sites, with the exception of M-FE (Table 2). Both CH and CL flower number per plant were independent of plant size in the latter site. There was an increase in the dependence of CH flower production on plant size at four of the five sites during the 1981 relative to the 1980 flowering season. Plant size continued to explain a significantly greater proportion of the variation in CL relative to CH flower production per plant, however, at the majority of sites (Table 2).

Significant between-site differences in the flower number-plant size relationships occurred for both flower types and years (Table 3). Chasmogamous flower number per plant was independent of plant size at site M-FE during both flowering seasons (Table 2). Relationships between CH flower number and plant size in the remaining sites, however, were more complex. Chasmogamous flower production was independent of plant size at sites SH-LE and SH-UF but dependent at sites M-HT and M-UF, although only an inconsequential proportion of variation in CH flower production was explained by plant size ( $r^2 = 0.04$  and  $r^2 = 0.02$ , respectively) at the latter

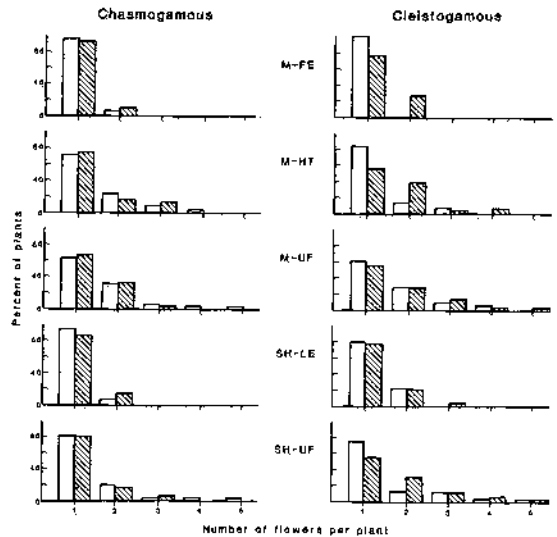


Fig. 2. Frequency distributions of the number of CH and CL flowers produced per flowering plant in 1980 (open bars) and 1981 (hatched bars).

sites. A significantly greater proportion of the variation in CH flower number, however, was explained by plant size at the four sites in 1981 ( $0.05 \leq r^2 \leq 0.19$ ). Between-site differences in the relationships between CL flower production and plant size differed significantly from those for CH flower number (Fig. 3, Table 3). Plant size explained a relatively higher proportion of the variation in CL flower number per plant at the predominantly deciduous upland forest sites, M-UF and SH-UF ( $r^2 > 0.21$ ), but a substantially lower proportion at sites SH-LE and M-HT ( $0.06 \leq r^2 \leq 0.12$ ) during both years of the study. In contrast, CL flower number per plant was independent of plant size at site M-FE in 1980 while in 1981 plant size explained a highly significant proportion of the variation in CL flower number ( $P < 0.01$ ,  $r^2 = 0.18$ ).

*Percent cleistogamy*—The relative production of CL and CH flowers is expressed here in terms of the percentage of all flowers produced at a site that were CL (Table 4). Chasmogamous and CL flower numbers per plant were too few (Fig. 2) to calculate values for comparison on a plant by plant basis. Percent cleistogamy ranged from 21.8 to 49.1% among sites in 1980 and from 37.9 to 71.2% in 1981 (Table 4). Between-site differences were highly significant ( $G = 8.2$ ,  $df = 4$ ,  $P < 0.01$ ). Percent cleistogamy was lowest (Table 4) and not significantly different among sites M-FE, M-HT, and SH-LE ( $G < 3.5$ ,  $df = 1$ ,  $P > 0.05$  for all pairs). Percent cleistogamy was highest in site

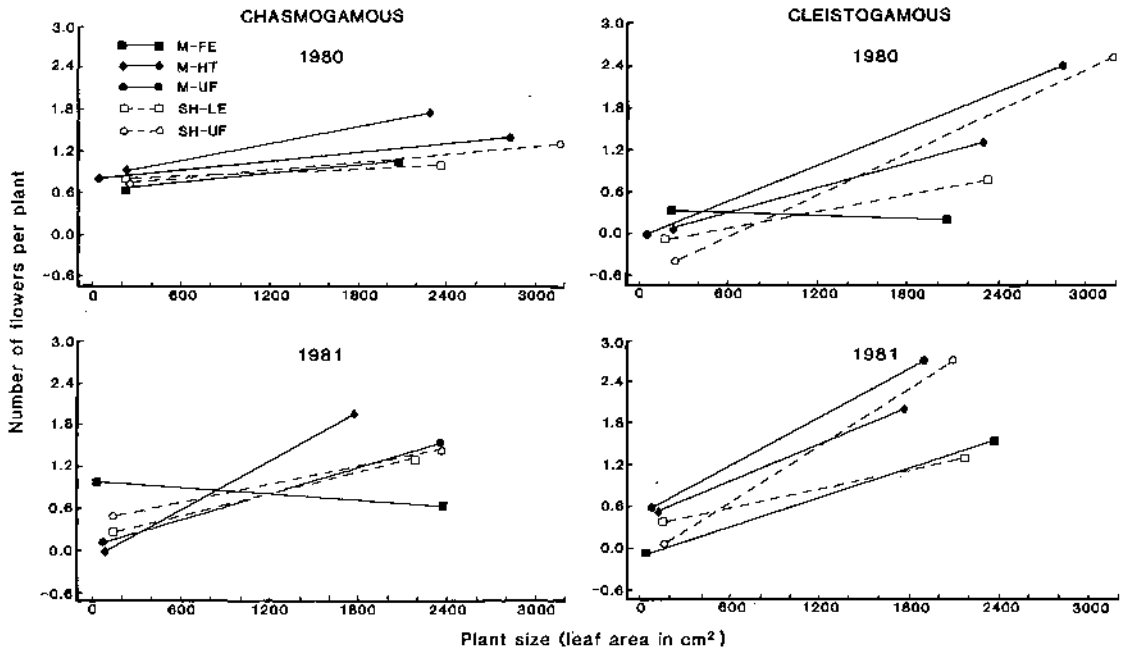


Fig. 3. The relationship between CH and CL flower number per plant and plant size (total leaf area) for each of the five forest sites during two flowering seasons. Values of the regression parameters and significance levels can be found in Table 2.

M-UF and intermediate in site SH-UF. The latter sites differed significantly from each other and all other sites ( $G > 6.0$ ,  $df = 1$ ,  $P < 0.05$ ). Between-year differences in the relative production of CH and CL flowers were also highly significant ( $G = 90.0$ ,  $df = 1$ ,  $P < 0.01$ ) and particularly striking. Percent cleistogamy increased markedly (by 13.5 to 30.7%) from 1980 to 1981 at the five sites. There was no significant interaction between site, year, and floral type ( $G = 4.2$ ,  $df = 4$ ,  $P > 0.05$ ).

**DISCUSSION**—In contrast to patterns of variation observed in other CL species, the degree of cleistogamy in *Oxalis montana* increased at sites with habitat conditions favoring plant growth and sexual reproduction and decreased at less favorable sites. The proportion of flowering plants producing CL flowers and the percentage of flowers produced at a site that were CL were highest at sites M-UF and SH-UF during the first year of the study (Tables 1, 4). Both sites were deciduous forest stands with luxuriant and diverse herbaceous understories indicating good growing conditions. Moreover, these sites had a high percentage of flowering plants of *Oxalis montana* (Table 1), and flowering plants produced, on average, higher numbers of CH and CL flowers than at other sites (Fig. 2). The degree of cleistogamy was lowest at sites M-FE and SH-LE which were

deeply shaded coniferous woods with a low diversity and abundance of understory herbs. The latter sites had a low percentage of flowering plants of *Oxalis montana*, and flowering plants produced few CH and CL flowers. Although site differences in cleistogamy and chasmogamy were not identical during the second flowering season, the degree of cleistogamy continued to be highest at the most productive and presumably best quality site, M-UF, and lowest at the least productive and poorest quality site, M-FE (Tables 1, 4).

Our results at first appear to contradict those obtained by Vereshchagina (1965) for the closely related European species, *Oxalis acetosella*. Vereshchagina (1965) reported that the percentage of CL flowers in populations was highest in densely shaded spruce woods which had low total flower production and lowest in sites with higher light intensity and more abundant flowering. Since CH and CL flowers were sampled only once in the four populations studied, these results are suspect. The timing and duration of CH and CL flowers in *Oxalis montana* (Fig. 1) indicates repeated sampling through the flowering season is necessary to obtain a reliable estimate of the relative production of the two floral forms in populations. This is particularly important with respect to CL flowers which are relatively few in number at any given sampling period but are produced

TABLE 2. Parameters and significance levels for the regressions of flower number on plant size in Fig. 3

Site	Year	Flower type	N	F	r <sup>2</sup>	a	b + SE (× 10 <sup>-3</sup> )
M-FE	1980	CH	40	1.28	0.03	0.66	0.20 ± 0.18
		CL	12	0.32	0.01	0.36	-0.10 ± 0.18
	1981	CH	38	0.61	0.01	0.96	-0.14 ± 0.18
		CL	20	10.42**	0.18	-0.13	0.70 ± 0.22
M-HT	1980	CH	91	4.82*	0.04	0.77	0.42 ± 0.19
		CL	40	14.34***	0.12	-0.09	0.59 ± 0.16
	1981	CH	33	12.64***	0.19	-0.13	1.17 ± 0.33
		CL	40	4.70*	0.08	0.44	0.86 ± 0.40
M-UF	1980	CH	161	4.14*	0.02	0.79	0.21 ± 0.11
		CL	151	60.87***	0.22	-0.03	0.85 ± 0.11
	1981	CH	111	34.71***	0.13	0.06	0.62 ± 0.11
		CL	216	71.44***	0.23	0.49	1.15 ± 0.14
SH-LE	1980	CH	46	0.33	0.01	0.83	0.08 ± 0.14
		CL	14	4.78*	0.09	-0.15	0.38 ± 0.17
	1981	CH	36	7.76**	0.12	0.14	0.54 ± 0.19
		CL	35	3.72*	0.06	0.28	0.45 ± 0.23
SH-UF	1980	CH	78	2.86	0.03	0.69	0.18 ± 0.11
		CL	52	55.40***	0.36	-0.66	0.99 ± 0.13
	1981	CH	78	6.80**	0.05	0.40	0.44 ± 0.17
		CL	83	50.88***	0.30	-0.18	1.33 ± 0.19

\*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ .

over a considerably longer duration than CH flowers (Fig. 1). Moreover, variation in the timing of CH and CL flower production evident among populations and years in both *Oxalis montana* and also in *Impatiens capensis* (Simpson, Alessio Leck, and Parker, 1985) demonstrates that sampling CH and CL flowers only once during a flowering season is likely to yield seriously biased estimates of the relative production of the two floral forms.

The degree of cleistogamy in other CL species has generally been found to increase under poor

habitat conditions, whether these be reduced light intensity (Schemske, 1978; Waller, 1980; Simpson et al., 1985), low soil moisture (Harlan, 1945; Brown, 1952; Koller and Roth, 1964; Waller, 1980), high plant density (Levin, 1972; Wilken, 1982; Cheplick and Quinn, 1983), or site disturbance (Campbell, 1982; Clay, 1983). Under these environmental conditions, resources and pollinators are more likely to be scarce and reproduction via cleistogamy is generally viewed as advantageous due to the reduced cost of production and the greater certainty of fertilization of CL relative to CH flowers (Schemske, 1978; Waller, 1979, 1980; Lord, 1981; Wilken, 1982; Schoen and Lloyd,

TABLE 3. Analysis of covariance: test for homogeneity of the regression relations in Fig. 3 between flower number per plant and plant size. Covariate = plant size. Years = 1980, 1981. Sites = M-FE, M-HT, M-UF, SH-LE, SH-UF. Flower types = CH, CL

Source of variation	df	MS	F
Plant size (total leaf area)	1	68.08	158.52***
Year	1	22.46	52.30***
Site	4	8.08	18.81***
Flower type	1	7.78	18.10***
Plant size × year	1	7.43	17.30***
Plant size × site	4	1.60	3.74***
Plant size × flower type	1	5.18	12.06***
Plant size × year × site	4	1.02	2.37*
Plant size × year × flower type	1	11.00	25.62***
Plant size × site × flower type	4	1.14	2.64*
Plant size × year × site × flower type	4	0.61	1.42
Error	1,348	0.43	

\*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ .

TABLE 4. Total CH and CL flower production and percent cleistogamy at each site during two flowering seasons\*

Site	Year	CH	CL	% CL
Montebello	1980	43	12	21.8
	1981	41	25	37.9
Hilltop	1980	135	49	26.6
	1981	47	63	57.3
Upland forest	1980	249	240	49.1
	1981	152	375	71.2
St. Hippolyte	1980	49	17	25.8
	1981	41	44	51.8
Upland forest	1980	95	75	44.1
	1981	104	141	57.6

\* Numbers of plants at each site are indicated in Table 1.

1984). Since reduced floral costs and increased seed production are associated with cleistogamy in *Oxalis* (Jasieniuk, in preparation), it is not immediately apparent why chasmogamy rather than cleistogamy should be the predominant mode of reproduction in *Oxalis montana* at relatively poor sites in contrast to the majority of CL species. A possible explanation lies in the influence of environment on the success of outcrossed versus selfed progeny. An increase in the relative production of CH progeny in sites with unfavorable growth conditions would be favored if outbred progeny have increased viability, fecundity, or both relative to inbred progeny in poor habitats. Heterosis in outcrossed progeny, for example, has been suggested to be expressed more strongly in harsher environments (Lloyd, 1980). Reductions in habitat quality, therefore, may have a greater negative effect on inbred than outbred progeny (Schemske, 1983) and favor CH reproduction in poor habitats. Since CH flowers in *Oxalis montana* are potentially outcrossing, the predominance of chasmogamy in poorer habitats may stem from such performance advantages of outcrossed progeny.

In several annual species with such mixed strategies of CH and CL flowering, the influence of habitat conditions on the balance of cleistogamy and chasmogamy is mediated largely through the effects of environment on plant growth and size (Waller, 1980; Wilken, 1982). Chasmogamous flowers dominate terminal and upper axillary inflorescences in these annual herbs while CL flowers are found among the lower axillary inflorescences (Lord, 1979; Waller, 1980; Weiss, 1980; Wilken, 1982), or on subterranean shoots (Schnee and Waller, 1986). Environmental conditions limiting growth produce small plants with few terminal branches and consequently few CH flowers. Favorable habitat conditions, in contrast, result in larger plants which produce an abundance of CH flowers in terminal inflorescences in addition to many CL flowers on axillary or subterranean branches. Hence CH reproductive effort has been observed to increase with plant size while CL reproductive effort remains relatively constant (Waller, 1980; Wilken, 1982; Schnee and Waller, 1986).

In contrast, plant size influenced the production of CL flowers to a greater extent than the production of CH flowers in *Oxalis montana* (Fig. 3; Tables 2, 3). Unlike previously studied annual herbs, *Oxalis* produces CH and CL flowers singly on peduncles arising from fleshy, petiole bases (Packham, 1978; Jasieniuk, personal observation). Hence the morphogenetic effects of plant size on CH and CL

floral development observed in annual species are unlikely to be responsible for the flower number-plant size relations in *Oxalis montana*. In contrast to other CL species, chasmogamy appears to form the predominant mode of reproduction in *Oxalis*, while reproduction via CL flowers increases when growing conditions are good and plants are, on average, larger in size (Fig. 4). Since CL flowers set a greater number of seeds and mature a larger seed biomass, on average, than CH flowers but are produced late in the growing season (Fig. 1) when resources are more likely to be scarce, it is possible that only plants growing in favorable habitats and reaching a larger size can incur the expense of maturing CL seed in addition to producing CH flowers and seed earlier in the growing season. Environmental factors such as water, light, and nutrients may exert effects on CH and CL flower production independent of plant size (Waller, 1980; Wilken, 1982) but our data does not allow partitioning the CL response into the direct effects of environment versus the indirect effects of environment on plant size.

We cannot determine whether genetic differences in reproductive response exist among populations of *Oxalis montana* with the data available. The similar ranking of sites on percent cleistogamy during two flowering seasons which differed markedly in the relative production of CH and CL flowers (Table 4), however, may be due to such genetically based differences. Genetic variation in the proportion of CH and CL flowers has been demonstrated previously in a number of species (Clay, 1982).

In addition to the significant spatial variation among sites in CH and CL flower production of *Oxalis montana*, there was also significant annual variation. Annual variation in CH and CL flower production by long-lived CL species has rarely been considered. We might expect that in a given habitat the balance of cleistogamy and chasmogamy would be fairly stable from year to year. This was not the case in *Oxalis*. The observed shift to greater CL reproduction during the second flowering season may have resulted from damage to floral buds or storage tissues during the unusually severe winter of 1980–1981 (Jasieniuk, 1985). Alternatively, depletion of resources in a year of high chasmogamy production may have induced a high proportion of cleistogamy in the subsequent year. Both this temporal variation in reproductive mode and the somewhat unusual patterns of spatial variation observed in *Oxalis montana* may be primarily associated with its perennial habit. Perennation provides



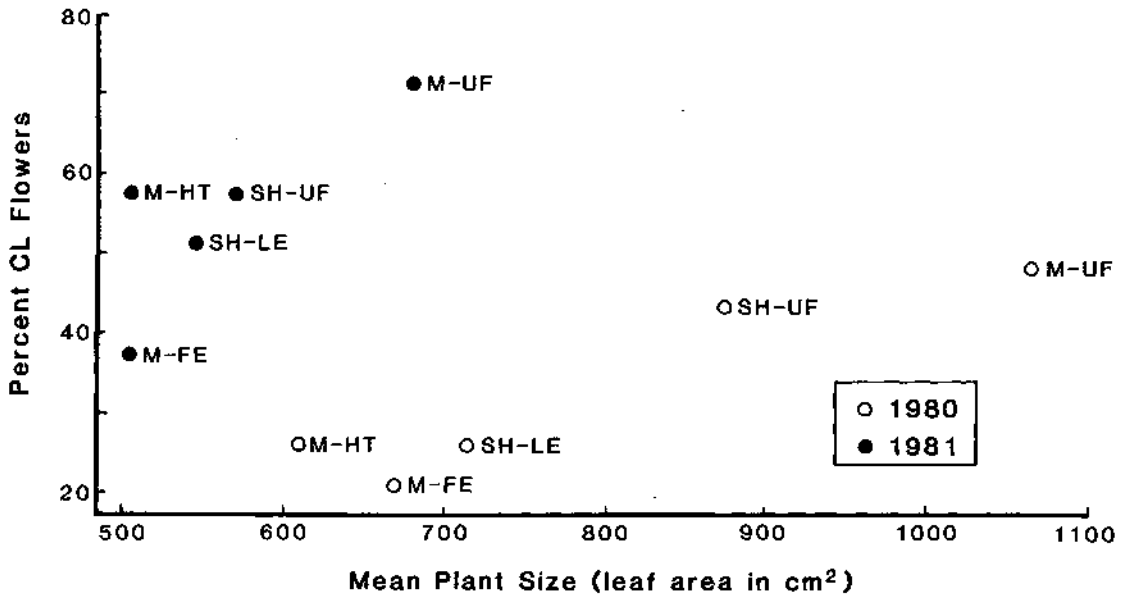


Fig. 4. Percent of all flowers in a local population that were cleistogamous plotted against the mean size of plants at each site during two flowering seasons. Site acronyms are given in the text.

opportunity for the use of stored resources, for example, in adjusting the balance of cleistogamy versus chasmogamy in spatially or temporally different environments. Further research is needed on the expression of cleistogamy in shade-tolerant forest perennials to determine the generality of the variation patterns observed.

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