Pollination ecology of five species in a limestone community

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ABSTRACT

Pollen was examined on the stigmatic surfaces of five species – *Campanula rotundifolia* L., *Euphrasia confusa* Pugsl., *Geranium robertianum* L., *Potentilla erecta* (L.) Rausch. and *Veronica chamaedrys* L. – sampled from a locality in North Yorkshire. Competition with blossoms of other species was found to adversely affect pollination in *Campanula rotundifolia* but enhance it in *Geranium robertianum*. Proportions of foreign pollen grains, observed on the stigmas of each species, correlate with the breeding systems of these species, being least where autogamy is involved.

INTRODUCTION

Beattie (1969) found that colonies of three species of *Viola*, growing in shaded habitats, had lower levels of pollination than those growing in more exposed habitats, and that an increase in the frequency of blossoms of other genera in the collection area resulted in the appearance of more foreign pollen grains within the stigmatic cavities of *Viola*. He also found that pollination did not differ markedly between habitats containing no blossoms of other genera and those containing many, but that large stands of conspicuous blossoms could monopolize the insect visitors in habitats shared by less eye-catching species, while habitats with a variety of blossoms could lure sufficient insects to ensure pollination of all species present. However, because *Viola* occurred with similar blossom densities throughout the habitats selected by Beattie, it was not possible for him to investigate the finding of Levin & Anderson (1970) that pollinators became less specialized in feeding behaviour as blossom density decreased and eventually fed with little discrimination between species.

For the present study, species were chosen that flower abundantly in August, and that differ from each other in size, colour and morphology of the flower. They were collected from sites that were readily accessible and showed a range of floristic differences within a restricted area.

The aims of this investigation were to see if blossom density per unit area acted as a major factor in pollination, to see how the presence of blossoms of other species affected pollination and to determine what factors seemed to influence the presence of foreign pollen grains.

MATERIAL AND METHODS

All material was collected at an altitude of 350 m from a limestone area near Malham, in the Craven District of North Yorkshire. Transects were laid across colonies of the species under investigation, and sub-colonies approximately 3 m in diameter were sampled at intervals of 5 m along the transect of *Geranium robertianum* L., and at intervals of 4 m on the transects of both *Potentilla erecta* (L.) Rausch. and *Euphrasia confusa* Pugsl. Populations of *Veronica chamaedrys* L. and *Campanula rotundifolia* L. were each sampled at two sites differing in the number of blossoms present within a unit area.

Fifty flowers were picked at random from each sub-colony of the first four species and 30 flowers from each sub-colony of *C. rotundifolia*. These were preserved in a viscous mixture of surgical spirit and glycerol (5:1), in order to minimize pollen movement between flowers. The flowers were picked at mid-anthesis, a condition recognized by fresh unwrinkled corollas and the degree of development

TABLE 1. MAJOR FLORISTIC FEATURES OF THE SAMPLE SITES

SPECIES	SAMPLE NUMBER	BLOSSOMS PER M^2	FREQUENCY OF BLOSSOMS, RECORDED WITHIN 5 M RADIUS (D, dominant; A, abundant; F, frequent; O, occasional; R, rare.)															DOMINANT PLANTS
			Urtica dioica	*Geranium robertianum*	*Mycelis muralis*	*Epilobium montanum*	*Ranunculus repens*	*Veronica chamaedrys*	*Thymus drucei*	*Potentilla erecta*	*Campanula rotundifolia*	*Cirsium* spp.	*Euphrasia confusa*	*Trifolium repens*	*Stellaria* sp.	*Hieracium* sp.	*Achillea millefolium*	
Geranium robertianum	G1	6	—	R	O	O	R	—	R	R	—	—	—	—	—	—	—	*Geranium robertianum*
	G2	11	F	O	O	—	—	—	—	—	—	—	—	—	—	—	—	
	G3	37	R	A	—	—	—	—	—	—	—	—	—	—	—	—	—	
	G4	22	—	F	O	—	—	—	—	—	—	—	—	—	—	—	—	
	G5	38	O	A	O	O	—	—	—	—	—	—	—	—	—	—	—	
	G6	7	—	R	O	—	—	—	—	—	—	—	—	—	—	—	—	
	G7	11	—	O	F	—	—	—	—	—	—	—	—	—	—	—	—	
	G8	4	—	R	O	—	—	—	—	—	—	—	—	—	—	—	—	
	G9	15	—	F	O	—	—	—	—	—	—	—	—	—	—	—	—	
	G10	7	F	R	—	—	—	—	—	—	—	O	—	—	—	—	—	
Potentilla erecta	P1	35	—	—	—	—	—	—	—	A	R	O	—	O	—	—	—	Gramineae
	P2	30	—	—	—	—	—	—	O	A	O	O	—	O	—	—	—	
	P3	5	—	—	—	—	—	—	—	R	—	O	—	—	—	—	—	
	P4	10	—	—	—	—	—	F	—	O	O	O	—	O	—	—	—	
	P5	3	—	—	—	—	—	R	—	R	R	—	—	R	R	F	—	
	P6	6	—	—	—	—	R	—	R	R	R	O	—	—	—	—	R	
	P7	4	—	—	—	—	R	—	R	R	R	O	—	—	—	—	R	
	P8	8	—	—	—	—	R	—	R	O	R	O	—	—	—	—	F	
	P9	2	—	—	—	—	F	—	R	R	R	O	—	—	—	—	R	

TABLE 1 (*continued*)

SPECIES	SAMPLE NUMBER	BLOSSOMS PER M^2	FREQUENCY OF BLOSSOMS, RECORDED WITHIN 5 M RADIUS (D, dominant; A, abundant; F, frequent; O, occasional; R, rare.)															DOMINANT PLANTS
			Urtica dioica	*Geranium robertianum*	*Mycelis muralis*	*Epilobium montanum*	*Ranunculus repens*	*Veronica chamaedrys*	*Thymus drucei*	*Potentilla erecta*	*Campanula rotundifolia*	*Cirsium* spp.	*Euphrasia confusa*	*Trifolium repens*	*Stellaria* sp.	*Hieracium* sp.	*Achillea millefolium*	
Euphrasia confusa	E1	10	—	—	—	—	—	—	—	—	—	—	R	—	—	—	—	Gramineae
	E2	20	—	—	—	—	—	—	—	—	—	—	O	—	—	—	—	
	E3	150	—	—	—	—	—	—	O	—	—	—	D	—	—	—	—	
	E4	100	O	—	—	—	—	—	—	—	—	—	D	—	—	—	—	
	E5	50	—	—	—	—	—	—	O	O	O	O	A	—	—	—	—	
	E6	25	—	—	—	—	—	—	—	O	O	O	F	—	—	—	—	
	E7	50	—	—	—	—	—	—	—	O	O	O	A	—	—	—	—	
	E8	15	—	—	—	—	—	—	R	O	—	O	O	—	—	—	—	
	E9	20	—	—	—	—	—	—	F	—	—	—	F	—	—	—	—	
	E10	60	—	—	—	—	—	—	R	—	O	O	A	—	—	—	—	
Veronica chamaedrys	V1	60	—	—	—	—	O	D	—	—	—	—	—	—	—	—	—	Gramineae
	V2	3	—	—	—	—	—	R	—	R	—	—	—	—	—	—	—	
Campanula rotundifolia	C1	6	—	—	—	—	—	—	—	—	O	—	—	—	—	—	—	Gramineae
	C2	1	—	—	—	—	—	—	O	F	R	—	—	—	—	—	—	

TABLE 2. POLLEN DATA FROM THE STIGMATIC SURFACES OF THE SPECIES INVESTIGATED

Species	Sample number	Number of stigmas with pollen			% Grains per sample		Grain numbers per stigma with pollen				
							Own		Foreign		
		Own only	Own & foreign	No pollen	Own	Foreign	Mean	80% Confidence limits (90% for totals)	Mean	Min.	Max.
Geranium robertianum	G1	33	0	4	100·0	0·0	10	2–23	—	—	—
	G2	15	1	28	99·3	0·7	9	1–28	1	1	1
	G3	19	0	13	100·0	0·0	6	1–14	—	—	—
	G4	19	0	12	100·0	0·0	7	1–19	—	—	—
	G5	24	5	5	95·6	4·4	12	1–47	3	1	5
	G6	20	3	10	89·2	10·8	7	1–21	6	1	16
	G7	23	0	10	100·0	0·0	4	1–13	—	—	—
	G8	24	0	11	100·0	0·0	9	1–21	—	—	—
	G9	30	1	5	99·8	0·2	14	1–33	1	1	1
	G10	34	1	16	99·5	0·5	8	1–20	1	1	1
	G Total	231	11	114	98·3	1·7	9	1–33	4	1	16
Potentilla erecta	P1	125	2	8	99·9	0·1	13	3–24	1	1	1
	P2	127	0	9	100·0	0·0	15	5–27	—	—	—
	P3	148	2	8	99·9	0·1	9	2–18	1	1	1
	P4	132	1	8	99·8	0·2	13	5–23	4	4	4
	P5	136	4	14	99·0	1·0	12	4–23	4	1	9
	P6	136	2	4	99·9	0·1	13	3–26	1	1	1
	P7	151	3	8	99·8	0·2	10	3–20	1	1	1
	P8	112	1	14	99·9	0·1	10	1–21	1	1	1
	P9	148	5	11	99·7	0·3	11	4–21	1	1	1
	P Total	1215	20	84	99·8	0·2	12	2–26	2	1	9

TABLE 2 (*continued*)

Species	Sample number	Number of stigmas with pollen			% Grains per sample		Grain numbers per stigma with pollen				
							Own		Foreign		
		Own only	Own & foreign	No pollen	Own	Foreign	Mean	80% Confidence limits (90% for totals)	Mean	Min.	Max.
Euphrasia confusa	E1	39	1	2	99·8	0·2	14	8–22	1	1	1
	E2	38	0	1	100·0	0·0	13	5–22	—	—	—
	E3	43	0	2	100·0	0·0	14	8–21	—	—	—
	E4	47	0	1	100·0	0·0	11	3–22	—	—	—
	E5	43	0	1	100·0	0·0	15	5–23	—	—	—
	E6	47	0	1	100·0	0·0	16	4–25	—	—	—
	E7	40	0	2	100·0	0·0	13	8–20	—	—	—
	E8	38	0	5	100·0	0·0	16	2–28	—	—	—
	E9	40	0	3	100·0	0·0	10	5–16	—	—	—
	E10	36	0	7	100·0	0·0	9	3–16	—	—	—
	E Total	411	1	25	100·0	0·0	13	3–25	1	1	1
Veronica chamaedrys	V1	32	3	3	98·6	1·4	10	2–21	2	1	2
	V2	29	3	4	99·1	0·9	11	2–21	1	1	1
	V TOTAL	61	6	7	98·8	1·2	10	2–22	1	1	2
Campanula rotundifolia	C1	3	11	0	87·8	12·2	62	20–95	10	1	21*
	C2	2	15	0	73·1	26·9	53	34–80	16	2	54
	C TOTAL	5	26	0	83·6	16·4	57	21–94	13	1	54

* 80% confidence limits used for *Campanula*

of the style. They were re-examined on these criteria in the laboratory prior to dissection. The style was subsequently removed and transferred to glycerine jelly, stained to the colour of claret by the addition of basic fuchsin. This mounting medium left stylar tissues yellowish green, but stained pollen grains red.

RESULTS

The stigmatic surfaces of all samples were examined for pollen. The pollen belonging to each species ('own' pollen) was readily distinguishable from grains of other species ('foreign' pollen) except for the pollen of *Euphrasia confusa* and *Veronica chamaedrys*, which Moore & Webb (1978) described as *Rhinanthus*-type. It was assumed that pollen of this type occurring on a stigma of either of these species belonged to that species, and therefore was not regarded as foreign pollen. Distinction between pollen of some other genera was not possible, notably those belonging to the Compositae. These grains were put in one of three categories – subfamily Cichorioideae, *Cirsium*-type and any other genera.

Floristic features of the collecting sites are summarized in Table 1. Pollen data are presented in Tables 2 and 3.

GERANIUM ROBERTIANUM

Percentage pollination and mean grain counts on stigmatic surfaces did not show significant differences (5% level) for different blossom densities of *Geranium robertianum*. High percentage pollination occurred in areas with many blossoms of other genera. Proximity of *Urtica* blossoms coincided with the occurrence of *Urtica* grains on the stigmatic surfaces of *Geranium*, but the presence of *Cirsium*-type pollen was not related to the proximity of suitable blossoms. The percentage of foreign pollen grains was generally below 1%, but in samples G5 and G6 it rose to 4·4% and 10·8% respectively.

POTENTILLA ERECTA

There was no significant difference (5% level) between mean grain counts per stigma at different blossom densities of *Potentilla erecta*. Four pollen types other than *Potentilla* were deposited on the stigmatic surfaces: *Cirsium*-type, Caryophyllaceae, Gramineae and an unknown pollen type, possibly a garden plant. Proximity of other blossoms reflected poorly in the pollen data. *Cirsium*-type pollen again occurred in an area with no blossoms of *Cirsium* nearby. Only one pollen grain from the Cichorioideae was found, although there were abundant *Hieracium* blossoms in site P5. Abundance of foreign blossoms was not reflected in the percentage pollination of *Potentilla*, which was high in all samples. The percentage of foreign pollen did not rise above 1%.

EUPHRASIA CONFUSA

Density of blossoms of *Euphrasia* did not correlate significantly with differences in percentage pollination or mean grain counts per stigma. Despite a variety of other blossoms along the transect, only one foreign pollen grain – *Cirsium*-type – was deposited on the stigma of *E. confusa*. It appears, therefore, that blossoms of other genera do not influence the pollination of this species.

VERONICA CHAMAEDRYS

Percentage pollination did not differ significantly between the two *Veronica* samples. More foreign grains, mainly of *Cirsium*-type, were recorded from site V1 (1·4%) than from site V2 (0·9%), but this difference was not significant at the 5% level.

CAMPANULA ROTUNDIFOLIA

100% pollination was observed in both samples of *Campanula* and mean pollen counts per stigma, both for own and foreign grains, were very high relative to the other species examined (significant at the 5% level). A twofold difference (not significant at 5%) in percentage foreign pollen occurred between the sites (12·2% at site C1 and 26·9% at site C2), due apparently to the presence of many *Potentilla* blossoms in site C2. The presence and identity of other foreign grains did not seem to correspond to nearby blossoms.

TABLE 3. FOREIGN POLLEN RECORDED ON THE STIGMATIC SURFACES OF THE SPECIES INVESTIGATED

Species	Sample number	Numbers of foreign grains per sample:	Gramineae	*Urtica*	*Epilobium*	*Potentilla*	*Rhinanthus*	*Cirsium*	Cichorioideae	Other Compositae	Caryophyllaceae	*Galium*	*Geranium*	Unknown type
Geranium robertianum	G1		—	—	—	—	—	—	—	—	—	—	—	—
	G2		—	1	—	—	—	—	—	—	—	—	—	—
	G3		—	—	—	—	—	—	—	—	—	—	—	—
	G4		—	—	—	—	—	—	—	—	—	—	—	—
	G5		—	—	—	—	—	16	—	—	—	—	—	—
	G6		—	—	—	—	—	19	—	—	—	—	—	—
	G7		—	—	—	—	—	—	—	—	—	—	—	—
	G8		—	—	—	—	—	—	—	—	—	—	—	—
	G9		—	—	—	—	—	1	—	—	—	—	—	—
	G10		—	1	—	—	—	—	—	—	—	—	—	—
Potentilla erecta	P1		1	—	—	—	—	1	—	—	—	—	—	—
	P2		—	—	—	—	—	—	—	—	—	—	—	—
	P3		1	—	—	—	—	1	—	—	—	—	—	—
	P4		—	—	—	—	—	—	—	—	1	—	—	3
	P5		—	—	—	—	—	15	1	—	—	—	—	—
	P6		—	—	—	—	—	2	—	—	—	—	—	—
	P7		2	—	—	—	—	1	—	—	—	—	—	—
	P8		—	—	—	—	—	1	—	—	—	—	—	—
	P9		—	—	—	—	—	5	—	—	—	—	—	—
Euphrasia confusa	E1		—	—	—	—	—	1	—	—	—	—	—	—
	E2		—	—	—	—	—	—	—	—	—	—	—	—
	E3		—	—	—	—	—	—	—	—	—	—	—	—
	E4		—	—	—	—	—	—	—	—	—	—	—	—
	E5		—	—	—	—	—	—	—	—	—	—	—	—
	E6		—	—	—	—	—	—	—	—	—	—	—	—
	E7		—	—	—	—	—	—	—	—	—	—	—	—
	E8		—	—	—	—	—	—	—	—	—	—	—	—
	E9		—	—	—	—	—	—	—	—	—	—	—	—
	E10		—	—	—	—	—	—	—	—	—	—	—	—
Veronica chamaedrys	V1		—	—	—	1	—	4	—	—	—	—	—	—
	V2		—	—	—	—	—	2	—	—	1	—	—	—
Campanula rotundifolia	C1		3	—	—	20	6	60	—	12	—	—	4	—
	C2		—	—	1	105	1	108	6	14	—	6	—	—

DISCUSSION

The presence of blossoms of other species in a habitat had different effects on pollination, depending upon the species in question. All species, with the exception of *Euphrasia confusa*, showed an increase in the number of foreign pollen grains related to the proximity and abundance of foreign blossoms. This supports Levin & Kerster's (1969) conclusion that pollinator behaviour and pollen dispersal are density dependent. The presence of foreign pollen on the stigma of a flower is evidence of potential cross-pollination. As *E. confusa* revealed only one foreign grain along the transect it seems likely that it is predominantly self-pollinated. The observations of Yeo (1966) also suggest that

self-pollination normally occurs in this species. Percentage pollination and the mean number of pollen grains on the stigmas of *Potentilla erecta* were high whether blossoms of other species were abundant or not, but large stands of other blossoms near *Geranium robertianum* increased the percentage pollination in *Geranium*. *G. robertianum* may therefore benefit from the presence of an apparent competitor which attracts more pollen vectors into the vicinity (see Thomson 1978). Competition for pollinators may be of reduced importance in late summer, since Lack (1982) reported an apparent saturation of insect visitors at this time of year. The reverse of the situation found in *Geranium* is apparent in *Campanula rotundifolia*, where apparent competition for pollinators with *Potentilla erecta* reduced the mean number of *Campanula* grains per stigma while greatly increasing the percentage of foreign pollen. Nevertheless, a relatively high pollen count was maintained due to the variety of visitors coming for food or shelter from the weather (Müller 1883, Knuth 1909).

Levin & Anderson (1970) claim that flower constancy breaks down as any pollinator visits progressively sparser populations of blossoms. If this is so one would expect to find the proportion of foreign pollen would increase as blossom density reduced. This relationship does not appear to exist in the species considered here, but it may be masked by local differences in abundance of other blossoms or by an insufficient reduction in blossom density, for although honey bees may have fixation areas of as little as 5 or 10 metres in favourable plant densities (Minderhoud 1931, Butler *et al.* 1943), their constancy to particular species may cause them to take more extended flights in diffuse colonies. Unfortunately little is known concerning constancy in Diptera and other non-Hymenopteran pollinators of the plant species considered.

The proportions of foreign grains present on the stigmas of the different species under investigation correlate well with the breeding systems of these species. Thus *Euphrasia confusa*, which appears to be essentially autogamous, had practically no foreign pollen, whereas *Campanula rotundifolia* and to a lesser extent *Veronica chamaedrys*, which are strongly outbreeding, attracted many foreign grains. *Potentilla erecta* and *Geranium robertianum* had few foreign grains and have breeding systems intermediate between the two extremes above.

The predominance and representation of Compositae in the foreign pollen of all species reflects the attractiveness of this type of blossom, its high pollen presentation and its successful competition for the pollen vectors of all the species studied. Knuth (1908) points out that visitors to *Cirsium* are both numerous and diverse and pollen of this type may be more susceptible than others to adhere to the body of an insect and to carry-over from previous forages due to its echinate exine ornamentation.

Separation of the effects of floristic composition, blossom density and other floral characters would have been clearer had sites been available in which more of these factors were constant, enabling direct comparisons between more similar sites. It would also be instructive to sample airborne pollen at blossom height in order to assess the importance of anemophilous transport of pollen in the pollination of these predominantly entomophilous species.

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