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Pollination biology of Apiaceae

Pushpa Koul, Namrata Sharma and A. K. Koul

Department of Biosciences, University of Jammu, Jammu 180 004, India

Members of the family Apiaceae exhibit diverse breeding systems ranging from completely selfed to obligately outcrossed. While the former is accomplished by the dehiscence of anthers above the stigma of the same flower, the latter is brought about through structural dioecy and gynodioecy. Majority of the species of Apiaceae are monomorphic and are either hermaphrodite or andromonoecious. In this article we review briefly the various strategies adopted by the members of Apiaceae to promote cross pollination by insects.

ALL members of Apiaceae have simple or compound umbel, and reproduce sexually. Despite uniformity in structure of inflorescence and flower, they exhibit diverse breeding systems, probably because of the wide variation in the mode of pollination. A whole range of pollination systems, varying from completely self- to obligate cross-pollination occur within the family.

Obligate outcrossing in umbellifers is imposed by structural dioecy and gynodioecy[1-3]. The dioecious species, e.g. *Aciphylla* and *Anisotome* bear male and female flowers on separate plants. In the gynodioecious taxa, e.g. *Gingidia*, *Scandia* and *Lignocarpa*, some plants carry female and others hermaphrodite flowers.

Taxa such as *Scandix pecten-veneris* which are completely self-pollinated represent the other extreme. Self-pollination is accomplished by dehiscence of anthers immediately above the stigma of the same flower[4]. That, such species are strictly autogamous is confirmed by the fact that the percentage seed set in bagged flowers is nearly equal to the control.

A few obligate self- or cross-pollinating taxa not withstanding, majority of umbellifers exhibit a blend of self- and cross-pollination. All such species are monomorphic but are either hermaphrodite or andromonoecious. In the former all flowers are bisexual whereas in the latter some flowers are staminate and others bisexual. Proportion of the two types varies in umbels of different orders of an individual (Table 1). The male flowers in andromonoecious species produce pollen of which only a small part is used in pollinating hermaphrodite flowers, the rest is used as reward to pollinators visiting the flower.

The monomorphic species employ different contrivances for promoting cross-pollination such as dichogamy. Umbellifers exhibit protogynous and protandrous type of dichogamy. The Himalayan species follow protandrous dichogamy. In this type, insects get dusted with pollen during the first phase of flowering and in the second, the stigmas are exposed for getting dusted in return. This alternation leads to cross-pollination. The magnitude of cross-pollination is determined by degree of protandry (Table 2, Figure 1).

In the strongly protandrous taxa, the male phase lasts in an umbel till the flowers continue to open. Once the opening of flowers is completed, the female phase begins abruptly in all flowers of the umbel[5-7]. In the weakly protandrous forms, namely *Torilis arvensis*, dehiscence of anthers of the inner flowers and receptivity of the stigmas of outer flowers within the umbel overlap leading to geitonogamy[8].

The phenological events in an individual are

Table 1. Percentage frequency of Hermaphrodite (H) and Male (M) flowers of different orders in andromonoecious umbellifers

Species	Umbel order I	II	III	IV	V	VI	Reference
Angelica venenosa	100	0	—	—	—	—	14
Anthriscus sylvestris	0	100	—	—	—	—	15
Conium maculatum	63.4	49.7	17.5	0	—	—	14
Coriandrum sativum	0	0	100				
Cultivar AH	53.93	38.48	30.13	26.33	25.02	23.57	7
M	46.07	61.52	69.87	73.67	74.93	76.43	7
Cultivar BH	82.72	65.89	45.71	40.04	20.36	14.04	7
M	17.28	34.11	54.29	50.06	79.64	85.96	7
Cultivar CH	67.74	39.27	25.78	20.53	—	—	7
M	32.26	60.73	74.22	70.47	—	—	7
Daucus carota ssp. *carota* H	96.62	65.47	36.50	26.77	0	—	9
M	3.38	34.53	63.50	72.28	100	—	9
D. carota ssp. *sativus* var *Pusa kesar* H	93.22	39.31	31.24	1.77	—	—	9
M	6.73	60.69	68.76	98.23	—	—	9
var. *sativa* H	92.67	32.34	33.17	26.41	2.31	—	9
M	7.33	67.66	66.83	73.59	97.69	—	9
Lomatium ambiguum H	4.33	50	51	—	—	—	16
M	96	67	50	49	—	—	16
L. bicolor var. *leptocarpum* H	1	55	76	94	—	—	16
M	99	45	2	36	—	—	16
L. canbyi H	6	52	63	—	—	—	16
M	94	48	37	—	—	—	16
L. cous H	3	44	44	54	—	—	16
M	97	56	56	46	—	—	16
L. farinosum var. *farinosum* H	9	51	69	70	73	—	16
M	91	49	31	30	27	—	16
var. *hambleniae* H	12	62	67	—	—	—	16
M	88	38	33	—	—	—	16
L. gayeri H	4	51	53	—	—	—	16
M	96	49	47	—	—	—	16
L. gormanii H	9	62	71	85	—	—	16
M	91	38	29	15	—	—	16
L. piperi H	14	71	86	—	—	—	16
M	86	29	14	—	—	—	16
Myrrhidendron donnellsmithii H	2.3	11.6	1.3	—	—	—	17
M	97.7	88.4	98.7	—	—	—	17
Pastinaca sativa H	87.40	45.80	0.90	0	—	—	15
M	12.60	54.20	99.10	100	—	—	15
Scandix pecten-veneris Morphoform AH	64.84	38.41	41.78	48.07	51.83	39.65	4
M	35.16	61.59	58.22	51.93	48.17	60.35	
Morphoform BH	55.46	42.87	48.97	58.33	—	—	4
M	44.54	57.13	51.03	41.67	—	—	
Syrnium olusatrum at Parys Moma mine H	50.10	34.00	11.80	3.50	—	—	15
M	49.90	66.00	88.20	96.50	—	—	
at Glanrafon H	67.63	0.31	8.6	0	—	—	
M	32.4	69.78	1.4	10	0	—	15
Torilis arvensis H	87.64	79.00	74.60	70.69	66.92	65.96	8
M	12.36	21.00	25.40	29.31	33.08	34.04	
Torilis leptophylla H	43.27	28.51	22.17	26.16	—	—	5
M	56.73	71.49	77.83	73.84	—	—	
T. japonica H	98.27	2.24	4.62	5.92	2.1	—	12
M	1.82	7.85	5.47	4.17	7.9	—	
T. nodosa H	100	100	100	100	98.39	6.1	12
M	0	0	0	0	1.7	3.9	
T. stocksiana H	100	100	97.4	95.89	2.9	83.1	12
M	0	0	2.6	4.2	7.1	16.9	

sequential. Flowers in the primary umbel bloom first followed by those of secondary, tertiary and quaternary umbels in that order. All umbels of the same order bloom simultaneously and only after they have all bloomed, do umbels of next higher order bloom[6]. Such sequential development of umbels of different orders

Table 2. Interval between dehiscence of anthers of flowers belonging to different orders

Taxa	Interval (in days) between dehiscence of anthers of flowers of I & II order	I & III order	III & IV order	Reference
Coriandrum sativum	1.5 ± 0.22	1.2 ± 0.2 (1–2)	1.25 ± 0.25 (1–2)	18 (1–2)
Daucus carota ssp. *carota*	3.8 ± 0.35 (2–7)	3.9 ± 0.31 (2–7)	—	6
D. carota ssp. *sativus* var. *Pusa kessar*	1.44 ± 0.2 (0–4)	22.28 ± 0.12 (1–3)	—	6
Var. *sativa*	2.92 ± 0.16 (2–4)	1.88 ± 0.16 (1–3)	—	6
Foeniculum vulgare ssp. *piperitum*	4.93 ± 0.33 (3–7)	4.4 ± 0.31 (3–7)	—	9
F. vulgare	4.9 ± 0.35 (2–8)	4.14 ± 0.57 (1–9)	—	9
Torilis arvensis	0.57 ± 0.53 (0–1)	0.37 ± 0.44 (0–1)	0	12
T. japonica	1.56 ± 0.18 (1–2)	1.75 ± 0.25 (1–3)	0.62 ± 0.18 (−1 to 2)	12
T. leptophylla	1.20 ± 0.13 (1–2)	0.60 ± 0.22 (0–2)	0.50 ± 0.19 (0–1)	12
T. nodosa	1.37 ± 0.18 (1–2)	1.14 ± 0.14 (1–2)	1	12
T. stocksiana	1.17 ± 0.21 (1–2)	1.33 ± 0.21 (1–2)	1.20 ± 0.20 (1–2)	12

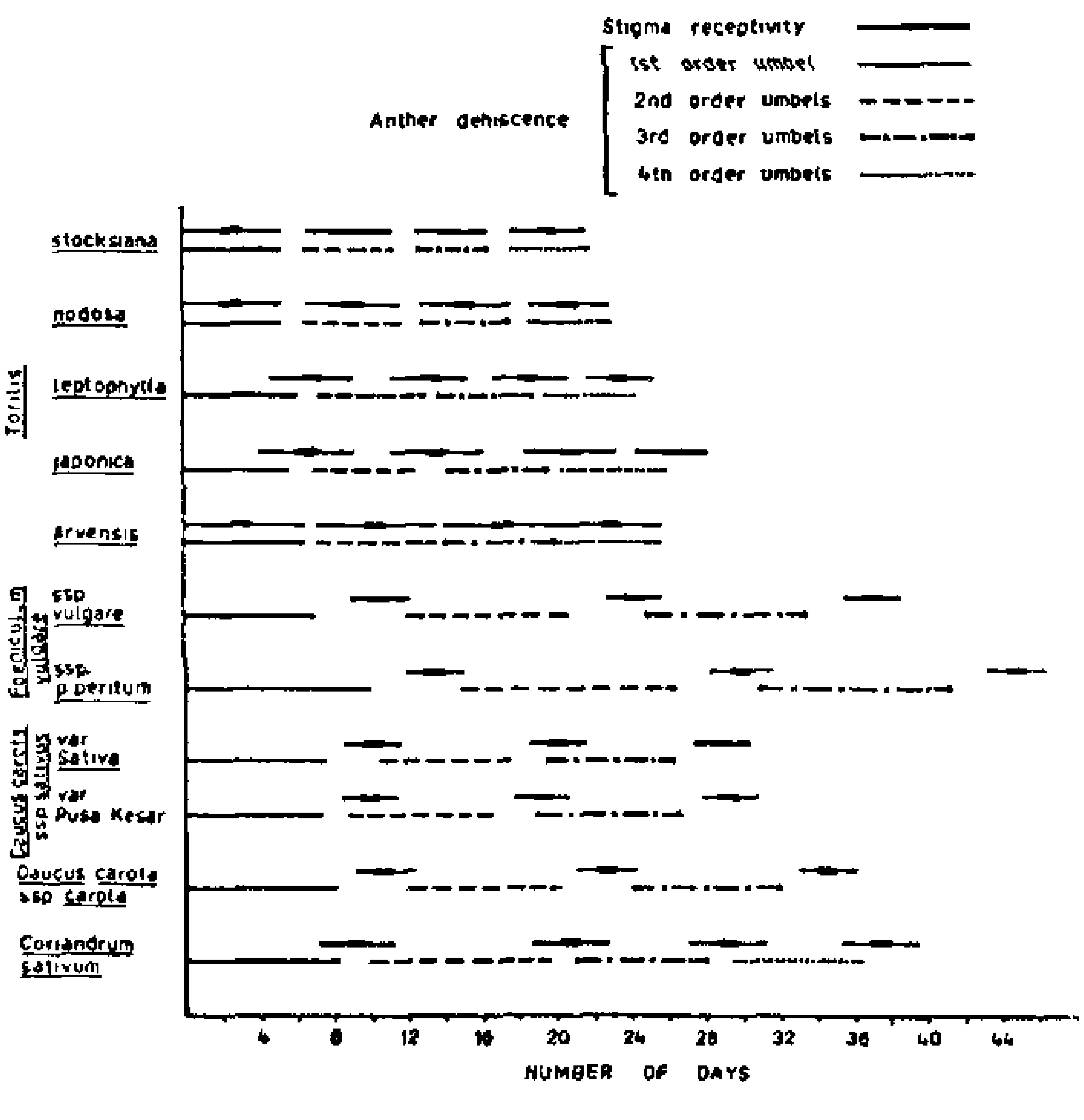

Figure 1. Diagrammatic representation of the temporal relation between anther dehiscence and stigma receptivity of the flowers of different umbel orders.

leads to overlap of male and female phases in such cases where the time gap between blooming umbels of two orders is narrow[9]. In taxa with no such overlap, selfing is precluded within a flowering shoot.

Pollen transfer in umbellifers is carried out by insects. Wind does not play any major role in their pollination. This is also brought out by the fact that very little of their pollen stays air borne[10,11]. Umbellifers are believed to exhibit 'promiscuous pollination' because of uniformity in floral structure. However, detailed studies undertaken during the last three decades have brought to light differences in finer details of umbel structure, with accompanying effect on pollination system. Although, individual flowers in Apiaceae are inconspicuous, their aggregation in umbels creates a strong visual impact and may function to attract insects. This is indirectly evident from our observation that umbel size is related to the mode of pollination. In those species which exhibit self-pollination, such as *Scandix pecten-veneris* and *Torilis stockesiana*, umbels are small and inconspicuous. On the contrary, umbels of the cross-pollinated species, such as *Daucus carota*, *Foeniculum vulgare*, *Torilis leptophylla*, etc., are large and quite conspicuous[9,11,12].

In *Coriandrum sativum*, *D. carota*, *Heracleum candicans* and others, flowers in the outer whorls of umbels are zygomorphic indicating their suitability to biotic pollinators[9,13]. Insect visitors to Umbels receive nectar and pollen as rewards. Nectar is secreted by the bulbous stylopodium. Nectar secretion commences early morning and continues up to 2 p.m. in *D. carota*, 2.30 p.m. in *F. vulgare* and 3 p.m. in *C. sativum*[11,13]. The quantity of nectar secreted during the receptive phase of stigma exceeds that secreted during anthesis. Thus against 0.05 μl of nectar secreted by a carrot flower for 2 h while anthers are dehiscing and pollen is available for insect consumption, the quantity secreted for the same period during receptive phase of stigma, when pollen is no more available, is 0.07 μl. It is argued that the difference in the quantity of nectar secreted by the flowers during the two developmental phases compensates for non-availability of pollen during the later stages.

The other reward that umbellifer flowers offer to visiting insects is pollen. An individual flower produces far more pollen than is required for fertilization of the two ovules in its ovary (see Table 3). The excess pollen may serve as reward to insect visitors. As the flowers of insect pollinated umbellifers open, they assume disc-shaped appearance with their nectariferous stylopodium lying exposed. Being easily available, the nectar and pollen attract a variety of insects to umbels. These include flies, bees, wasps, ants, beetles and some hemipteran insects[9,11-13].

Insect visits to umbels is influenced by extrinsic factors, particularly light and temperature. Dipterans constitute the bulk of visitors to fields of *D. carota* ssp. *sativus* (97.14 per cent on sunny days. However, on cloudy days, hymenopterans outnumber other insects including dipterans (41.22 per cent hymenopterans and 39.86 per cent dipteran insects). In contrast, plants of *D. carota* are visited more frequently by hymenopteran (72–84 per cent on sunny day and 49.44 per cent on cloudy day) than dipteran insects[9]. This difference is, in all probability, caused by the difference in flowering periods of the two taxa. Their flowering overlaps only for a brief period during which the quality of pollinators on umbels of both taxa is alike suggesting, among other things, the non-specificity of pollinators. In carrot as well as fennel, maximum number of insects visit umbels from early morning up to 2 p.m. In coriander, insect activity is at peak around noon[13]. Umbellifers are visited by a variety of insects. Hymenopterans and dipterans constitute bulk of visitors to umbels of wild as well as cultivated carrot and fennel[9,11]. Coleopteran and hemipteran insects are not efficient pollinators. Hymenopterans, which constitute 5 per cent and 64–72 per cent visitors to cultivated and wild forms of *D. carota* carrying 33 per cent and 97 per cent pollen of the cultivated and wild forms respectively. Hymenopterans constitute 84 per cent of the total visitors of cultivated and 94 per cent to wild forms of *F. vulgare* and carry 97 and 98 per cent pollen load, respectively. Finally, for the pollination of *C. sativum* and species of *Torilis* also, hymenopterans are rated as most efficient pollinators[12,13].

Table 3. Pollen–ovule ratio per hermaphrodite flower and per individual

Taxa	P/O ratio	
	per flower	per plant
Coriandrum sativum	3464:1	9793:1
Daucus carota ssp. *carota*	4957:1	8943:1
D. carota ssp. *sativus*		
var. *sativa*	3925:1	8298:1
var. *Pusa kesar*	5060:1	10397:1
Foeniculum vulgare ssp. *piperitum*	14635:1	14635:1
F. vulgare ssp. *vulgare*	12005:1	12005:1
Scandix pecten-veneris	1246:1	2774:1
Torilis arvensis	903:1	1038:1
T. japonica	2956:1	5632:1
T. leptophylla	2650:1	9883:1
T. nodosa	793:1	830:1
T. stocksiana	633:1	663:1

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