An experimental study of hybridization between *Heracleum mantegazzianum* Somm. & Levier and *H. sphondylium* L. subsp. *sphondylium* (Umbelliferae)

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ABSTRACT

Experimental crosses were made on material of *H. mantegazzianum* and *H. sphondylium* subsp. *sphondylium* (Umbelliferae) obtained from south-eastern Scotland. The interspecific cross was successful, but only when *H. sphondylium* was the maternal parent. Self-pollination within an umbel was not usually successful because of protandry, but self-pollination of flowers of the primary umbel of *H. mantegazzianum* with pollen from the secondary umbel was successful. The progeny from these crosses were observed over four years. Hybrid crosses gave rise to intermediate progeny, which resembled putative hybrids from the field. *H. sphondylium* was perennial though not long-lived; *H. mantegazzianum* was monocarpic, taking three to five years to flower; longevity and flowering in the hybrid was generally intermediate.

INTRODUCTION

Putative hybrids between *Heracleum mantegazzianum* Somm. & Levier and *H. sphondylium* L. have recently been described in detail from several sites in south-eastern Scotland (Grace & Stewart 1978; Stewart 1979). These plants, morphologically intermediate between the presumed parent species, are not numerous, but can be found where *H. mantegazzianum* and *H. sphondylium* grow interspersed. A study of male meiosis at one mixed *Heracleum* site has demonstrated the certain hybrid nature of these plants, which are virtually sterile (Weimarck *et al.* 1979). The low fertility of the hybrids is probably due to differences in the karyotypes of *H. mantegazzianum* and *H. sphondylium* which cause segregational aberrations at meiosis in the hybrid. Although there was no evidence for introgression at sites studied in south-eastern Scotland, incidental occurrence of backcrossing is probable (Weimarck *et al.* 1979).

H. mantegazzianum was introduced from the Caucasus and subsequently became naturalized in Britain in the 1800s (Stewart 1979). Thus the geographical barrier between *H. mantegazzianum* and *H. sphondylium* has been reduced. Observations on flowering time and the pollen load of insect visitors at a mixed *Heracleum* site in Scotland (Grace & Nelson 1980) have shown that, although the species have a more or less distinct insect fauna, some insect species visit both species of *Heracleum* and so a small amount of pollen is transferred between them.

The work reported in this paper was designed to determine whether hybrids could be synthesized by experimental transfers of pollen between the parent species.

MATERIALS AND METHODS

Experimental crosses were made on individuals of *H. mantegazzianum* and *H. sphondylium* subsp. *sphondylium* obtained from several sites in south-eastern Scotland (Table 1). The plants were removed from the field in March or early April 1977, before the rosette of leaves had reached 0·5 m diameter, planted in 0·18 m³ plastic tubs containing the plants' own soil and brought to Edinburgh. Less than 50% of the transplants produced suitable flowering shoots. Some remained in a vegetative state (none of the hybrid transplants flowered) and some were badly damaged by the larvae of *Depressaria pastinacella* Duponchel (Parsnip Flat-bodied Moth) which lays its eggs on unopened umbels of *Heracleum* (Thompson & Price 1977; Thompson 1978). Plants used for experimental crosses were moved into a cool glasshouse early in June. Floral development was observed on the

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TABLE 1. ORIGINS OF PLANT MATERIAL MENTIONED IN THE TEXT.

Overall, less than 50% of transplants survived and fewer flowered

Site name and number of transplants	Grid reference	Code numbers of plants used in experimental crosses
Farfield (20)	36/262.632	21,22,24–26,29,31,32,36–39
Hopetoun (10)	36/093.788	41–45, 48–50
Park Burn (7)	36/308.678	40
Riddell (10)	36/519.247	51
Roslin (10)	36/270.627	
Stobs (10)	36/506.100	2,5,7

primary and secondary umbels of the plants in the glasshouse (umbel nomenclature follows Lovett Doust (1980)).

Flowers for experimental crosses were emasculated as petals unfurled, using fine forceps to strip off anthers before they had dehisced. To prevent accidental pollination, umbellets of *H. mantegazzianum* and umbels of *H. sphondylium* were enclosed in paper bags made of lens tissue (Shepherd 1975) sealed on three sides with 'Sellostic' or 'Pritt' adhesive and tied at the open end. Flowers were pollinated after an interval of one to three days by gently brushing a dehisced anther across the receptive stigma surface.

For each type of cross at least 70 flowers (140 stigmas) from a primary umbel were used. *H. mantegazzianum* had sufficient flowers in the single terminal umbel for at least one of each of the four types of cross:

1. Self: using pollen from the same plant as the stigma.
2. Outcross: using pollen from a different plant of the same species (intraspecific cross).
3. Hybrid: using pollen from a plant of a different species (interspecific cross).
4. Control: flowers emasculated but not pollinated.

Since *H. sphondylium* could accommodate only one cross and control in a primary umbel the type of cross was allocated at random to individual flowering shoots from the same plant. Pollen for outcrosses was obtained from primary umbels cut from *H. sphondylium* growing at Roslin and *H. mantegazzianum* of Park Burn provenance, grown outside the Department of Forestry and Natural Resources, University of Edinburgh. Self-pollination, using pollen from secondary umbels, was attempted with *H. mantegazzianum* only.

Dried mericarps were harvested and stored at room temperature. For seed counts, mericarps were passed over a light table and those with at least 2/3 by volume of developed endosperm were scored as 'seed set', as, when dissected, such individuals contained apparently healthy embryos.

All seed from the experimental crosses was set out to germinate on sterile agar plates at 2–5 °C in the dark (Stewart 1979). At two-week intervals plates were checked and seeds which had the tip of the radicle exserted were counted as germinated and removed to seed trays on the glasshouse mist bench to develop cotyledons. Three seedlings of each of the self and outcrosses and five seedlings of each of the hybrid crosses were grown on to young plants and transplanted to a cultivated field at Farfield (Table 1) in the summer of 1978.

A record was kept of the number of plants flowering, vegetative or dead from 1979 to 1982. The height of each plant was measured at one-week intervals from 30th May to 1st August 1979, and the number of rays counted on plants flowering in 1980.

RESULTS

FLORAL DEVELOPMENT

H. sphondylium flowered from 19th June to 11th July 1977, *H. mantegazzianum* from 28th June to 4th July 1977. The development of individual hermaphrodite flowers of *H. sphondylium* and *H. mantegazzianum* is illustrated in Fig. 1. Most flowers opened in the early morning, anthers dehisced
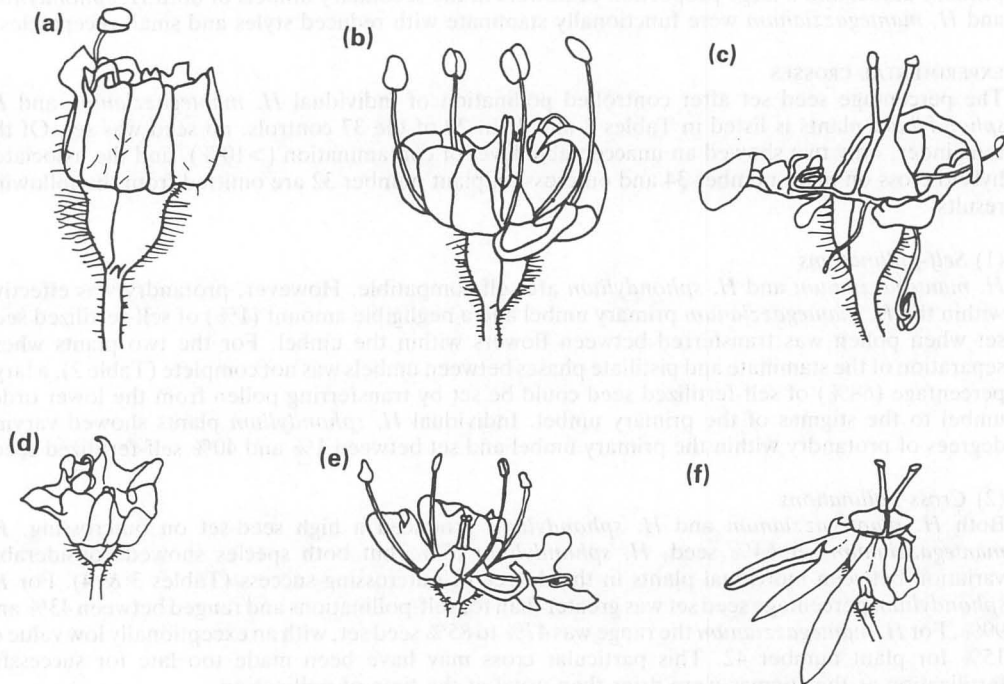
FIGURE 1. Floral development in *H. mantegazzianum* (a–c) and *H. sphondylium* (d–f). The three stages, from left to right, are buds (a & d), dehiscence (b & e) and receptive stigmas (c & f). Style lengths and standard deviations: *H. mantegazzianum* 2·11 ± 0·49 mm, *H. sphondylium* 1·58 ± 0·23 mm.

between 7 and 9 a.m., and filaments had collapsed by the following day. Individual flowers opened in sequence from the outer flowers of outer umbellets to the central flowers of central umbellets, usually over five days. This staminate phase of the umbel was followed by an interval of one to three days before all flowers became receptive across the umbel on the same day. While the flower was receptive the stigma and indumentum surface were moist; after fertilization the surfaces dried out, and the fruit began to elongate. Flowering in the primary umbel was followed by flowering in secondary umbels, and then in tertiary umbels. The length of the staminate phase and the interval of flowering between different order umbels in the experimental plants are shown in Table 2. Although there appeared to be complete protandry within an umbel, the staminate and pistillate phases on some plants overlapped between primary and secondary umbels. Flowers in the centre of the

TABLE 2. DURATION IN DAYS OF STAMINATE PHASE AND INTERVAL BETWEEN FLOWERING IN PRIMARY AND SECONDARY UMBELS (MODE AND RANGE) AND NUMBER OF PLANTS WITH OVERLAP BETWEEN STAMINATE AND PISTILLATE PHASES IN DIFFERENT UMBELS

	H. sphondylium	*H. mantegazzianum*
Number of plants observed	23	9
Duration (days) of staminate phase in primary umbel:	4,5 (3–7)	5 (3–6)
Interval (days) between staminate phase in primary and secondary umbels:	3 (0–7)	2 (1–4)
Number of plants with overlap between staminate phase in secondary and pistillate phase in the primary umbel:	2	2
Number of plants with overlap between staminate and pistillate phase in separate primary umbels:	11	0

primary umbel and a large proportion of flowers in the secondary umbels of both *H. sphondylium* and *H. mantegazzianum* were functionally staminate with reduced styles and small receptacles.

EXPERIMENTAL CROSSES

The percentage seed set after controlled pollination of individual *H. mantegazzianum* and *H. sphondylium* plants is listed in Tables 3 and 4. In 20 of the 37 controls, no seed was set. Of the remainder, only two showed an unacceptable level of contamination (>10%), and the associated hybrid cross on plant number 34 and outcross on plant number 32 are omitted from the following results.

(1) *Self-pollinations*

H. mantegazzianum and *H. sphondylium* are self-compatible. However, protandry was effective within the *H. mantegazzianum* primary umbel and a negligible amount (1%) of self-fertilized seed set when pollen was transferred between flowers within the umbel. For the two plants where separation of the staminate and pistillate phases between umbels was not complete (Table 2), a large percentage (68%) of self-fertilized seed could be set by transferring pollen from the lower order umbel to the stigmas of the primary umbel. Individual *H. sphondylium* plants showed varying degrees of protandry within the primary umbel and set between 1% and 40% self-fertilized seed.

(2) *Cross-pollinations*

Both *H. mantegazzianum* and *H. sphondylium* produced a high seed-set on outcrossing. *H. mantegazzianum* set 64% seed, *H. sphondylium* 67%, but both species showed considerable variation between individual plants in the degree of outcrossing success (Tables 3 & 4). For *H. sphondylium* percentage seed set was greater than for self-pollinations and ranged between 43% and 99%. For *H. mantegazzianum* the range was 47% to 85% seed set, with an exceptionally low value of 15% for plant number 42. This particular cross may have been made too late for successful fertilization as the stigmas were drier than usual at the time of pollination.

(3) *Hybrid pollinations*

The hybrid cross with *H. mantegazzianum* stigmas set only 2% seed overall, a level which could not be declared statistically greater than that of the unpollinated controls. Ultimately, these seeds gave rise to mature plants that were indistinguishable from the maternal parent, and so it was concluded that the 2% seed set had indeed been the result of accidental pollination. Thus, these individuals will not be considered further. In comparison, the hybrid cross with *H. sphondylium* as female parent was successful, and overall a 23% seed set was obtained (Tables 3 & 4). Despite the variation between individual plants, a statistical analysis of the seven *H. sphondylium* plants with all three treatment types showed that the difference in seed set attributed to cross type was significant ($F=18.43$, $P<0.001$). For *H. sphondylium* it was possible to set more seed from a hybrid pollination than by selfing within the primary umbel, although the greatest amount of seed was set by cross-pollination.

(4) *Seed germination*

Nearly all seed set by *H. sphondylium* plants had germinated after 22 weeks (Table 5). There was no distinct difference between the final germination percentages for seeds from any one cross type or plant provenance, as the number of seed germinating from any one seed batch was very variable. However, seed from the hybrid cross began germinating 2 weeks earlier at 9 weeks and continued more rapidly with a maximum at 17 weeks.

H. mantegazzianum seed began germination earlier, at 7 weeks, and reached a maximum at 15 weeks. Overall, only about half of the experimentally-produced seed germinated.

SURVIVAL AND GROWTH OF THE FIRST GENERATION FROM EXPERIMENTAL CROSSES

The first generation of hybrids from the *H. sphondylium* × *H. mantegazzianum* cross was easily distinguished. The plants were larger, with more rays in the primary umbel (Fig. 2), and grew more rapidly than *H. sphondylium* (Fig. 3). In stem diameter and number of rays they were indistinguishable from the presumed hybrids described elsewhere (Weimarck *et al.* 1979). Many of the hybrids showed structural weakness and abnormal flower development with sterile anthers,

TABLE 3. PERCENTAGE SEED SET AFTER CONTROLLED POLLINATION OF INDIVIDUAL
H. MANTEGAZZIANUM PLANTS

Plant Number	Self-pollination		Cross-pollination		Hybrid pollination	
	No. of flowers pollinated	Percentage seed set	No. of flowers pollinated	Percentage seed set	No. of flowers pollinated	Percentage seed set
41	72 (96)*	6 (64)*	57	85	108	1
42	75	0	81	15	88	0
43	79 (86)*	(73)*	81	72	90	0
44	75	0	80	69	88	1
45	77	0	80	56	81	1
48			82	76	79	0
49	86	0	92	83	81	0
50	84	0	76	47	71	0
51	83	4	84	77	83	15
MEAN		1 (68)*		64		2

* Self pollination of primary umbel with 2° umbel pollen

TABLE 4. PERCENTAGE SEED SET AFTER CONTROLLED POLLINATION OF INDIVIDUAL
H. SPHONDYLIUM PLANTS

Plant Number	Self-pollination		Cross-pollination		Hybrid pollination	
	No. of flowers pollinated	Percentage seed set	No. of flowers pollinated	Percentage seed set	No. of flowers pollinated	Percentage seed set
2					114	51
5			98	67		
7	224	3				
21	243	5	158	55	80	10
22	122	10	78	78	78	4
24	138	8	100	48	133	18
25	150	4	88	99	118	38
26	349	30	211	70	240	24
29			124	70		
31	110	1	98	59	98	13
32	114	33			163	17
35	110	6			97	9
36	100	25			75	47
37			80	88	83	13
38	125	14	92	77		
39	83	29			150	22
40 (1)	128	40	88	43	84	23
MEAN		16		68		22

TABLE 5. TOTAL GERMINATION (PERCENT) AFTER 22 WEEKS AT 2 °C

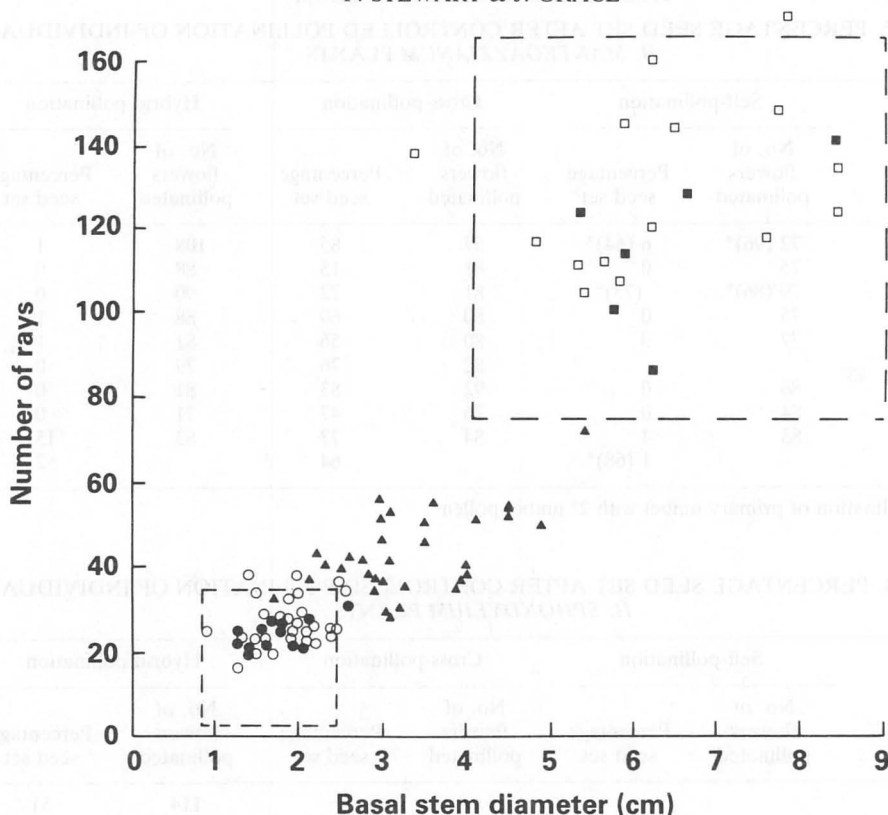|	Self	Outcross	Hybrid
H. sphondylium	91	91	73
H. mantegazzianum	27	59	—

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FIGURE 2. Scatter diagram to show relationships between different types of cross. ■, *Heracleum mantegazzianum* selfed; □, *H. mantegazzianum* outcross; ●, *H. sphondylium* selfed; ○, *H. sphondylium* outcross; ▲, hybrid cross with *H. sphondylium* the maternal parent. The large rectangles made of broken lines denote the range of stem diameter and number of rays recorded in the field from pure populations of *H. sphondylium* and *H. mantegazzianum*.

stunted styles and contorted developing fruit, in contrast with *H. sphondylium* and *H. mantegazzianum* which flowered normally. The hybrids survived at least as well as the selfed and outcrossed progeny, though they had a greater tendency than *H. sphondylium* to remain vegetative, with most individuals remaining vegetative for one or more years out of four (Fig. 4). *H. mantegazzianum* flowered in its third, fourth or fifth year and generally died afterwards. Most hybrids did not die after flowering (Fig. 4).

DISCUSSION

HYBRIDIZATION

An entry in Stace (1975) and the previous notes of McClintock (1973) provide the only published description of the hybrid *H. mantegazzianum* × *H. sphondylium*. Reference to a probable hybrid in the field was made by Praeger (1951) for Ireland, and Perring & Walters (1964) for two sites in Cambridgeshire; Kent (1975) listed several sites for the putative hybrid in Middlesex, where M. G. Collet and R. K. Brummitt recorded the hybrid along the banks of the River Brent near Ealing in 1962 and 1967. Specimens collected in 1969 by P. H. Davis and C. W. Muirhead, from a mixed *Heracleum* population growing in the centre of Edinburgh, were sent to the Russian authority I. P. Mandenova and were returned with the comment "Il est bien probable que c'est une forme hybride". Possible hybrids have also been collected by R. K. Brummitt from a colony near Heathrow
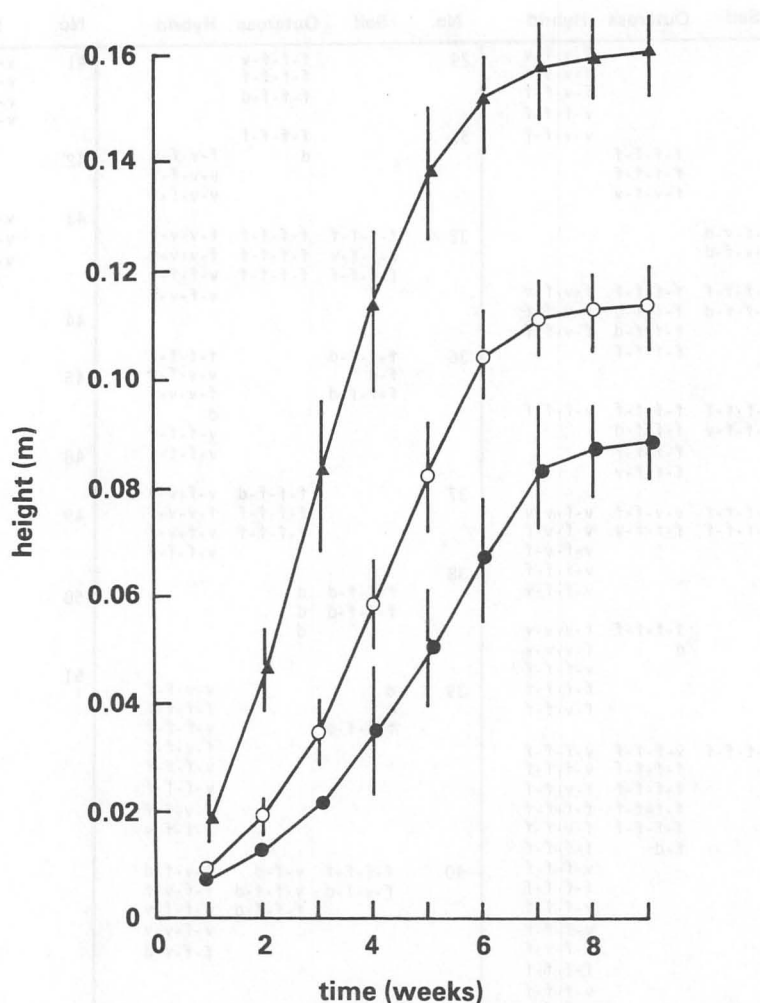
FIGURE 3. The growth in height of *H. sphondylium* progeny which flowered in 1979. ▲, interspecific hybrids; ○, outcross; ●, selfed. Bars denote 95% confidence limits.

(Stace 1975) and by D. McClintock from Coldstream in south-eastern Scotland. Also in Scotland, records have been made at the Black Isle (Muirhead 1974), Caithness (McClintock 1973) and in Morayshire (McCallum Webster 1978). We have found putative hybrids of *Heracleum* at most sites where the species grow together (Grace & Stewart 1978). They are nearly sterile and intermediate in all characters measured, including certain microscopic features of the leaf surface (Weimark *et al*. 1979; Arora *et al*. 1982). The work reported in this paper shows that hybrids may be artificially synthesized with remarkable ease, as long as *H. sphondylium* is the maternal parent, and that these hybrids are indistinguishable from presumed hybrids in the field.

The incidence of hybrids of *Heracleum* species in the field is low in relation to the ease with which they may be synthesized. This is mainly due to the extremely selective foraging behaviour of insects (Grace & Nelson 1981), a clear case of ethological isolation, similar to that reported in *Antirrhinum* (Mather 1947) and *Papaver* (McNaughton & Harper 1960). The low incidence of hybrids, together with their low fertility, probably accounts for the lack of any marked introgression, and means that

Panel 1

No.	Self	Outcross	Hybrid
2			f-v-f-v
			f-v-v-f
			f-v-f-f
			v-f-f-f
			v-v-f-f
5		f-f-f-f	
		f-f-f-f	
		f-v-f-v	
7	f-f-v-d		
	f-v-f-d		
21	f-f-f-f	f-f-f-f	f-v-f-v
	f-f-f-d	f-f-f-d	f-v-f-f
		f-f-f-d	f-v-f-f
		f-f-f-f	
22	f-f-f-f	f-f-f-f	v-f-f-f
	f-f-f-v	f-f-f-d	
		f-f-f-f	
		f-f-f-v	
24	f-f-f-f	v-v-f-f	v-f-v-v
	f-f-f-f	f-f-f-v	v-f-v-f
			v-f-v-f
			v-f-f-f
			v-f-f-v
25		f-f-f-f	f-v-v-v
		d	f-v-v-v
			v-f-f-f
			f-f-f-f
			f-v-f-f
26	f-f-f-f	v-f-f-f	v-f-f-f
	d	f-f-f-f	v-f-f-f
	d	f-f-f-f	f-v-f-f
		f-f-f-f	f-f-f-f
		f-f-f-f	v-f-f-f
		f-d	f-f-f-f
			v-f-f-f
			f-f-f-f
			v-f-f-f
			v-f-f-f
			f-f-v-f
			f-f-f-f
			v-f-f-f
			v-f-f-v

Panel 2

No.	Self	Outcross	Hybrid
29	f-f-f-v		
	f-f-f-f		
	f-f-f-d		
31	f-f-f-f		f-v-f-v
	d		v-v-f-f
			v-v-f-f
32	f-f-f-f	f-f-f-f	f-v-v-v
	v-f-f-v	f-f-f-f	f-v-v-v
	f-f-f-f	f-f-f-f	v-f-v-v
			v-f-v-f
36	f-f-f-d		f-f-f-f
	f-d		v-v-f-f
	f-f-f-d		f-v-v-f
			d
			v-f-f-f
			v-f-f-f
37		f-f-f-d	v-f-v-v
		f-f-f-f	f-v-v-f
		f-f-f-f	v-f-f-f
38	f-f-f-d	d	
	f-f-f-d	d	
		d	
39	d		v-v-f-f
	d		f-f-f-f
	f-f-f-d		v-f-f-f
			f-v-f-f
			v-f-f-f
			v-f-f-f
			f-v-f-f
			v-f-f-v
40	f-f-f-f	v-f-d	f-v-f-d
	f-v-f-d	v-v-f-d	f-v-f-f
		f-f-f-d	v-f-f-v
			v-f-v-v
			f-f-v-d

Panel 3

No.	Self	Outcross
41	v-v-f-d	v-v-f-d
	v-v-f-d	v-v-f-d
	v-v-v-v	v-v-v-v
	v-v-f-d	
42		v-v-f-d
		v-v-f-d
43	v-v-v-v	v-v-f-d
	v-v-f-d	v-v-f-d
	v-v-f-d	v-f-d
		v-v-f-d
44		v-f-d
		v-f-v-d
45		v-v-v-f
		v-v-f-f
		v-v-f-d
48		v-v-f-d
		v-v-f-d
49		v-v-f-d
		v-v-f-d
		v-v-v-f
50		v-f-d
		v-f-d
		v-f-d
51		v-v-v-f
		v-f-d
		v-f-d

FIGURE 4. Observations on the flowering of progeny 1979–1982. Plants 2–40 were *H. sphondylium*, 41–51 were *H. mantegazzianum*. v, plant remained vegetative; f, plant flowered; d, plant dead. Thus v-f-f-d, for example, would mean that the plant was vegetative for one year, flowered for two years and then died.

hybridization cannot in this case be considered to be very significant in evolutionary terms. There can, however, no longer be any doubt as to whether hybrids do occur.

It remains of great interest to see whether hybridization can occur between the numerous other heraclea found in the Caucasus, which, like *H. sphondylium* and *H. mantegazzianum*, all have a diploid chromosome number of 22 (Grossheim 1967). The cytogenetic and chemotaxonomic relationships between the European subspecies of *H. sphondylium* are already under investigation (Weimarck 1978; Weimarck & Nilsson 1980).

Heracleum is not the only genus in the Umbelliferae in which an experimental cross has been successful at the interspecific level. McCollum (1975) has made crosses between *Daucus carota* and *D. capillifolius*, and also between *D. gingidium* and the cultivated carrot (McCollum 1977). These crosses, along with the several reports of putative hybrids in other umbelliferous genera (Stace 1975)

suggest that the view expressed at two successive international conferences, that "hybridization is almost unknown in the family" (Bell 1971; Heywood 1978), should now be abandoned.

BREEDING SYSTEMS

Most members of the Umbelliferae are protandrous, the exceptions being *Hydrocotyle, Sanicula* and *Erigenia* (Bell 1971). Protandry itself is unlikely to guarantee outcrossing, as pollination by the anthers of adjacent flowers within the umbel might occur. However, the entire umbel of *H. sphondylium* is nearly protandrous, with stigmas becoming receptive only after most of the anthers on the umbel have withered (Proctor & Yeo 1973). When self-pollination was achieved, as in the pollination of primary umbels with pollen from the secondary umbels, the seed set was quite high and germination as effective as from an outcrossing. However, the progeny displayed inbreeding depression: they did not grow as tall as the outcrossed progeny, were more often dead after five years, and those surviving were often puny with few flowering stems per plant. It seems that self-pollination involving the secondary umbel may be unusual, though of great potential importance in the case of a founder plant which happens to be remote from other sources of pollen.

The failure of the hybrid cross when *H. mantegazzianum* was the maternal parent may result from the excessive style length of the giant species. Similar cases are mentioned in Stace (1975), and the rather limited observations that could be made in the present work support this view.

LONGEVITY

According to the *Flora Europaea* account of *Heracleum*, *H. sphondylium* is a biennial or a short-lived perennial, whereas *H. mantegazzianum* is biennial, monocarpic, or perennial (Brummitt 1968). The present observations show that *H. sphondylium* does not usually display biennial behaviour, and is not particularly short-lived – more than half the plants survived for five years. *H. mantegazzianum* never displayed 'true' biennial activity, but was usually monocarpic, taking three, four or five years to flower. This may be partly the result of the rather exposed nature of the site, since true biennial activity has been observed previously when material was planted in a sheltered plot. On the other hand, casual observations in the wild suggest variable longevity. There are now several studies which show that 'biennial' plants may take a number of years to complete their life cycle, depending on the competitive relationships within the plant community (Holt 1972; Werner 1975). It is also known, again by casual observation, that *H. mantegazzianum* will flower a second time if it is cut down before the flowers have opened, as often happens when half-hearted attempts to eradicate it from public places are made. The only other recorded information on flowering in the genus is the observations made on *H. sibiricum* by Rabotnov (1956): this species remains vegetative for one or more years and then blooms sporadically, dying after 13 to 15 years.

The life cycle may be related to the ecological niche which the species occupy. In Britain, *H. mantegazzianum* is an opportunist, rapidly colonising bare ground on river banks after a flood, producing much seed with a high germination rate, and rapidly becoming locally dominant (Clegg & Grace 1974). *H. sphondylium*, on the other hand, produces fewer seeds which germinate over a longer period, and plants co-exist with other species at a relatively low population density, for example in ruderal habitats (Way 1979), and in certain tall-herb communities on mountains (McVean & Ratcliffe 1962).

The longevity of the hybrid is surprising, as many individuals are mechanically unstable and consequently display somewhat contorted or even prostrate forms of growth. Observations at Kale Water in southern Scotland suggest that the hybrid in the field is not particularly long-lived: most of those sampled by us in 1977 have now (1982) gone and others have appeared.

HYBRIDIZATION AND WEED CONTROL

Heracleum mantegazzianum is a troublesome weed, which is spreading both in Britain (Clegg & Grace 1974) and in North America (Morton 1978). Not only is it invasive, but also its sap causes photosensitization of human skin to ultra-violet components of solar radiation. This results in painful burns, a condition known as phytophotodermatitis (Drever & Hunter 1970). The active principles of the sap are 6, 7- furocoumarins, known as psoralens (Eichstedt Nielsen 1971). Although the weed can be adequately controlled using a commercial herbicide based on glyphosate, it has been suggested that *H. mantegazzianum* could be 'hybridized out of existence' by encouraging gene exchange between *H. mantegazzianum* and *H. sphondylium*. It now seems unlikely that this could

ever be achieved. Quite apart from the considerable difficulty of obtaining a suitable pollen vector, and the uncertainty regarding the photoxicity of the hybrid sap, the unilateral compatibility reported in this paper is not in the desired direction. The outcome of massive random pollen transfers would be to transfer genes from *H. mantegazzianum* to *H. sphondylium* and not vice versa, hence exacerbating the problem of phototoxicity, and perhaps causing unwanted evolutionary change in a familiar native plant.

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