

## DISPERSAL STRATEGIES IN THE APIACEAE: THE TEMPORAL FACTOR AND ITS ROLE IN DISSEMINATION

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### Abstract

The study has been aimed at finding the significance of the time factor in the dynamics of seed dispersal in the Apiaceae. For this purpose, a computerized Data Base of the Israeli Apiaceae was constructed, and field investigations and population censuses were carried out. Four spatial types of dispersal could be recognized in the 94 Israeli species: Anemochorous (26%), Zoochorous (31%), Hydrochorous (2%), Autochorous and Barochorous (41%). From the temporal aspect, three general quantitative modes of dissemination could be defined: (i) Prompt dissemination (common in annuals); (ii) gradual; (iii) totally retarded, plus a multiple-mode type, i.e. strategy of alternative modes combined (e.g. heterocarpy). Within the gradual mode, three principal temporal patterns of dissemination were discerned: Short-time continuous, bi-sequential (double-peaked), perpetual and truncated. Prolongation or delay of the dispersal period are regulated in the Apiaceae by various mechanisms, particularly by phenological-developmental characters and morpho-anatomical features, sometimes affected by extrinsic climatic factors. Associations between life forms, spatial dispersal categories and temporal modes are described. Similar temporal modes may occur in different categories, yet there are some correlations between spatial dispersal types and temporal patterns. The time factor contributes to the variability in dispersal strategies. The delay may have an adaptive value since it affords either a longer period of dispersal or/and higher rates of seed-flow.

### Introduction

Dispersal - i.e., the movement of a plant's diaspore from one place to another - is a major system of gene flow which plants employ to reach new niches, where a new generation can be established (LEVIN & KERSTER, 1974; LEVIN, 1981). The dispersal process is thus a main factor in the geographical distribution of species and it both affects and is affected by population structure. Four main spatial dispersal types, determined on the basis of the dispersing agents, were recognized and widely described (e.g., RIDLEY, 1930; ZOHARY, 1937; PIJL, 1982; BERG, 1983): Anemochory, Hydrochory, Zoochory and Autochory. In contrast to fruit structural and spatial types, which have been intensively investigated, the temporal or dynamic aspects have received relatively little attention.

The timing of dispersal, viz. the timing and rates of discharge of diaspores from the parent plant, has been discussed mainly in connection with seeds' survival in arid areas (e.g., ELLNER & SHMIDA, 1981; ARONSON & AL., 1990; STEINBERGER & al., 1990). The phenomenon of delay has been associated with dormancy of seeds. It is considered a 'biological clock' controlling the germinability following rainfall events. From an ecological perspective, such mostly in-situ or anti-telechory dispersal



(ZOHARY, 1962) was regarded as a mode to reach the reproductive maximum in randomly varying environments (e.g., COHEN, 1966; COHEN, 1976; ZEIDE, 1978; VENABLE & LAWLOR, 1980). Some other studies deal with the phenological changes in fruit development, as ecologically related to Ornithochory (e.g., THOMPSON & WILLSON, 1979; WILLSON & THOMPSON, 1982), or to animal-fruit interactions in general (JANZEN, 1983).

This study has been aimed at finding the significance of the time factor throughout the dispersal phase: from the stage of maturation of the diaspore on the mother plant, through the discharge stage, to the stages of direct transport, fixation and establishment. Our studies were focused on the duration and rate of the dissemination. We have assumed that the timing and rates of the discharge of diaspores are adaptive characters, involved in more than a single ecological aspect (e.g., successful transport in an environmentally suitable period, decreasing the risk of predation, increasing the chances and efficiency of dispersal). Our hypothesis was that since dispersal is a multi-phase process in time, as well as in space, then distinct temporal variations, perhaps diverse modes, will be recognized within the whole adaptive strategy. For this purpose, field studies were carried out during May-November 1994, in which the dissemination of twenty species of *Apiaceae* was regularly examined. Most of the other species of the family in Israel were checked in field during 1994-1995, in order to outline preliminary indications on the temporal patterns and modes of their dispersal.

The family *Apiaceae* is characterized by simple, dry, indehiscent fruit, namely a schizocarp. It consists of two carpels that split when mature along the middle into two, one-seeded indehiscent mericarps (DRUDE, 1897-1898; HEYWOOD, 1968; HEYWOOD, 1978). These normally remain for some time suspended from a common forked stalk, the carpophore. All the species share a basic anatomical structure of the fruit itself. The carpophore may play a significant role in dispersal (mainly in the subfamily *Apioideae*), being responsible for the duration of the mericarps' attachment to the mother plant and the timing and the rate of their discharge. The structure of the carpophore was investigated from the anatomical-morphological point of view (JACKSON, 1933; FAHN & WERKER, 1972; FAHN, 1990: 499-503), but its functional adaptations to environmental conditions are still unclear. A quite remarkable variability in fruit morphology is known in the *Apiaceae*, expressed in variations in surface, shape, size and colour of the fruit (THEOBALD, 1971; HEYWOOD, 1978). Yet, from the aspect of dispersal in space, the roughly 3000 species of this family are basically quite restricted in their adaptations to the dispersal vectors: no fleshy fruits occur; all fruits consist of indehiscent two, one-seeded, mericarps similar in their anatomy; the range of size and weight is rather limited relatively to other large plant families. This physical uniformity and the fact that numerous species grow in the Mediterranean territory of Israel, were the reasons why we have chosen the *Apiaceae* for our investigations of the temporal factor in dispersal.



## Methods

### Botanical material

A computerized Data Base of the *Apiaceae* of Israel was prepared, based on literary data (ZOHARY, 1972; FEINBRUN-DOTHAN & DANIN, 1991, HELLER & HEYN, 1993), field observations and records maintained by the authors, and information retrieved from herbarium specimens deposited at the HUJ. This Data Base includes detailed notes on taxonomy, life forms, habitats, distribution, floral and fruit characteristics and updated phenological records. A special emphasis was placed on classification of the fruit types according to various characters, including mericarp dimensions, and fruit shape or structure, and ecological-spatial modes of dispersal.

Ninety-four Umbellifers are recorded in Israel (after excluding extinct, confused, cultivated species and adding three new ones, Appendix 1). The subfamily *Apioideae* contains the major part of these (87 spp.), and most of its tribes are represented in our flora (Fig. 1a). The family in Israel is characterized by mostly ephemeral species, many annuals (53%, Fig. 1b), growing chiefly in open and sunny habitats. Several species inhabit cultivated fields and disturbed areas; tumbleweeds are relatively common (9 spp.). Most of Israeli *Apiaceae* (89%) are distributed in the Mediterranean territory of the country, while the others are exclusive to deserts or the semidesert steppes.

### Sites and field studies

Two study sites were located near Jerusalem, 3 km apart, both in the natural Mediterranean ecosystem. The first site (iHar Herzlî) is 800 m a.s.l., with open terraces sustaining low shrubby or herbaceous vegetation. The second site ("Hadassa") is 600 m a.s.l., with open suppressed maquis and large herbaceous clearings. Each site covers an area of 10,000 m<sup>2</sup>. The study area is in the Judean Mountains district, characterized by temperate Mediterranean climate, in which the average annual precipitation is 550-600 mm (ROSEMAN, 1970).

Twenty *Apiaceae* species (see Appendix 1) were recorded at both sites (site one: 16 spp.; site two: 12 spp.). Five individuals of each species, more than 5 m apart from one another, were labeled during the blooming season. Observations and measurements of dissemination have been carried out from March to November 1994, weekly in the first two months, later once in 2-3 weeks. Firstly the maturation or ripening dates were recorded; in this stage all the well-developed mericarps were scored. From the start of mericarps falling, the number of the remainders per plant was counted, every visit. Through this procedure, we could figure out the rates of dissemination in time. Besides the detailed examination of the selected plants, comparisons with all the other plants at the site and with the same species and other Israeli Umbellifers occurring at other locations were performed as well. The temporal types of other Israeli Umbellifers, which do not occur in the study sites, were determined by analogy to the observed types. The resulted frequencies were subjected to X<sup>2</sup> tests (contingency tables).



## Results

### Mericarps and diaspores

Within most of the studied species, the single mericarp (in *Apioideae*) or the whole fruit (in *Hydrocotyloideae* and *Saniculoideae*) are functioning as a diaspore. The dispersal unit is separated from the plant after maturation during the dry season. In 15 species (16%) in Israel, the diaspore is the whole plant, and the fruits do not detach from their carpophore or pedicel. Within the latter group, most of the perennial species have an abscission tissue formed at the stem base (FAHN, 1990) and the whole plant may be distributed by the wind as a tumbleweed (e.g., *Ferula biverticillata*, *Prangos ferulacea*, *Hippomarathrum boissieri* and *Eryngium maritimum*). The annuals, in contrast, are dislocated from the ground only by the Fall whirlwinds (e.g., *Scandix palaestina* and *Capnophyllum peregrinum*).

Fruit size of 80% of the species is less than 10 mm long. There is a weak trend ( $P = 0.09$ ,  $X^2$  test) towards small-sized (1-3 mm) mericarps in annuals (22 ssp.) and large fruits (more than 10 mm) in perennials (11 ssp.)

### Spatial dispersal modes

The distributions of the four principal spatial dispersal modes according to life forms, fruit size, fruit shape, and fruit structure, are summarized in Table 1 and Fig. 1.

Mode	number of species	Life-form		Fruit size			Fruit shape					Features of fruit					
		A-B	H-C	small	medium	large	I	II	III	IV	V	A	B	C	D	D	
Anemoruche	29	10**	19**	(4)0	(15)12 <sup>x</sup>	(10)8 <sup>x</sup>	6	2	20	4	-	19	5	1	6	1	
Zoochorous	24	19**	5**	7	14 <sup>x</sup>	3	21	2	1	-	-	1	-	1	6	16	
Autochorous	39	24	15	23 <sup>x</sup>	10	6	24	7	2	-	6	28	2	-	9	-	
Hydrochorous	2	1	1	2	-	-	2	-	-	-	-	2	-	-	-	-	
Totals	94	54	40	[1]		[2]		53	11	23	4	6	50	7	2	21	17

$x^2$  test: difference from expected value significant at \*\*)  $P \leq 0.01$ , x)  $P \leq 0.1$ .

Table 1. Distribution of Spatial dispersal modes in Israeli *Apiaceae* according to Life-forms, and size, shape and features of fruit. Life form: A-B, annuals & biennials; H-C, hemicryptophytes & chamaephytes. Fruit size: Small, up to 3 mm; Medium, 3-10 mm; Large, more than 10 mm. Fruit shape: I, spherical or ovoid; II, cylindrical; III, compressed and wing-like; IV, balloon-like; V, long linear (beaked). Features of fruit: A, surface smooth and ribbless; B, surface rough or tubercled or sticky; c, diaspore plumed or comose; D, surface hairy; E, spiny or bristly. [1], 9 tumbleweeds excluded from the "fruit-size" category; [2], 3 species with fruit dimorphism were counted twice.



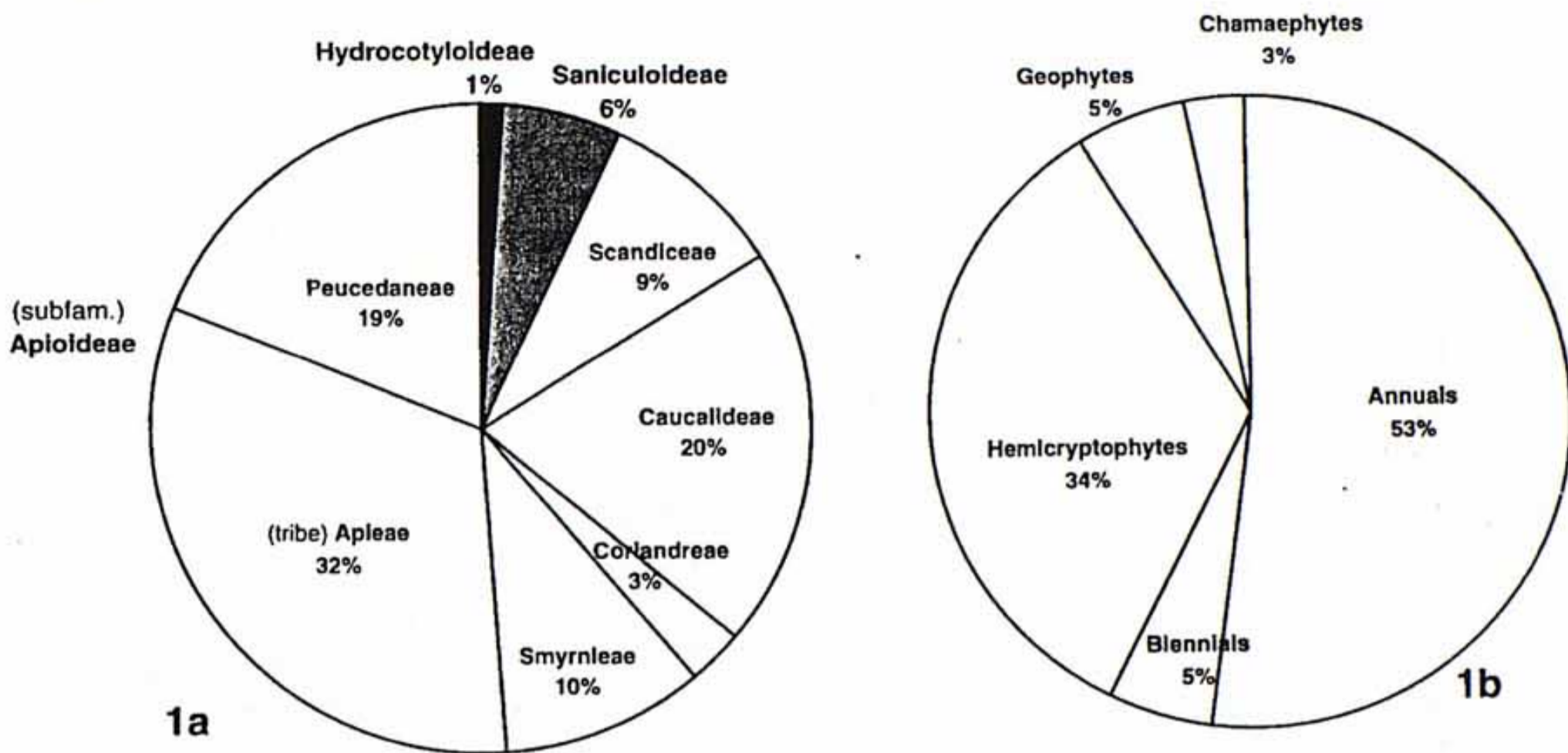


Fig. 1. Distribution of Israeli *Apiaceae* according to taxonomic classification (1a) and life forms (1b).

Despite the multi-modal situation in several species, in the analyses we have taken into consideration only the principal mode. Autochory is the common mode (42%), equally distributed among the life-form categories, but significantly more common in plants with small and smooth mericarps. Anemochory (31%) and Zoochory (26%) pertain to most of the other species. Anemochory is significantly associated with perennial species, relatively large-sized, smooth and wing-like mericarps, whereas the small-sized fruits are absent in this category. Zoochory is significantly associated with annuals, ovoid and spiny mericarps, equally distributed among the fruit-size classes. Hydrochory occurs actually in only two species (*Hydrocotyle ranunculoides* - by floating mericarps, and *Exocantha heterophylla* - by hydrochastic mechanism after rain).

### Reproductive Cycles and Phenology

The annual blooming cycle of the Israeli *Apiaceae* is presented in Figure 2. Like most species of Israeli flora, which flower during the brief spring (ZOHARY, 1962), the peak of the *Apiaceae* flowering is in April-May (80% of all species). The termination of the potential dispersal season is determined by environmental factors - the Fall rains and winds during November. Therefore, the potential dispersal season of most Israeli species stretches from the end of the rainy months to the first rains of the next year when seeds can germinate, a time span of 7-8 months. The duration of fruit maturation is relatively constant, approximately 3-5 weeks. It is therefore possible to determine the beginning of fruit dispersal from the flowering date. The transportation of seeds, both directly from the mother plants and indirectly by carry-over, takes place during May-November, duration of 170-200 days, depending on the ecological situation in the particular year. The early blooming species have the maximum potential dispersal time, but 85% of the species disperse their diaspores within 5-6 months.



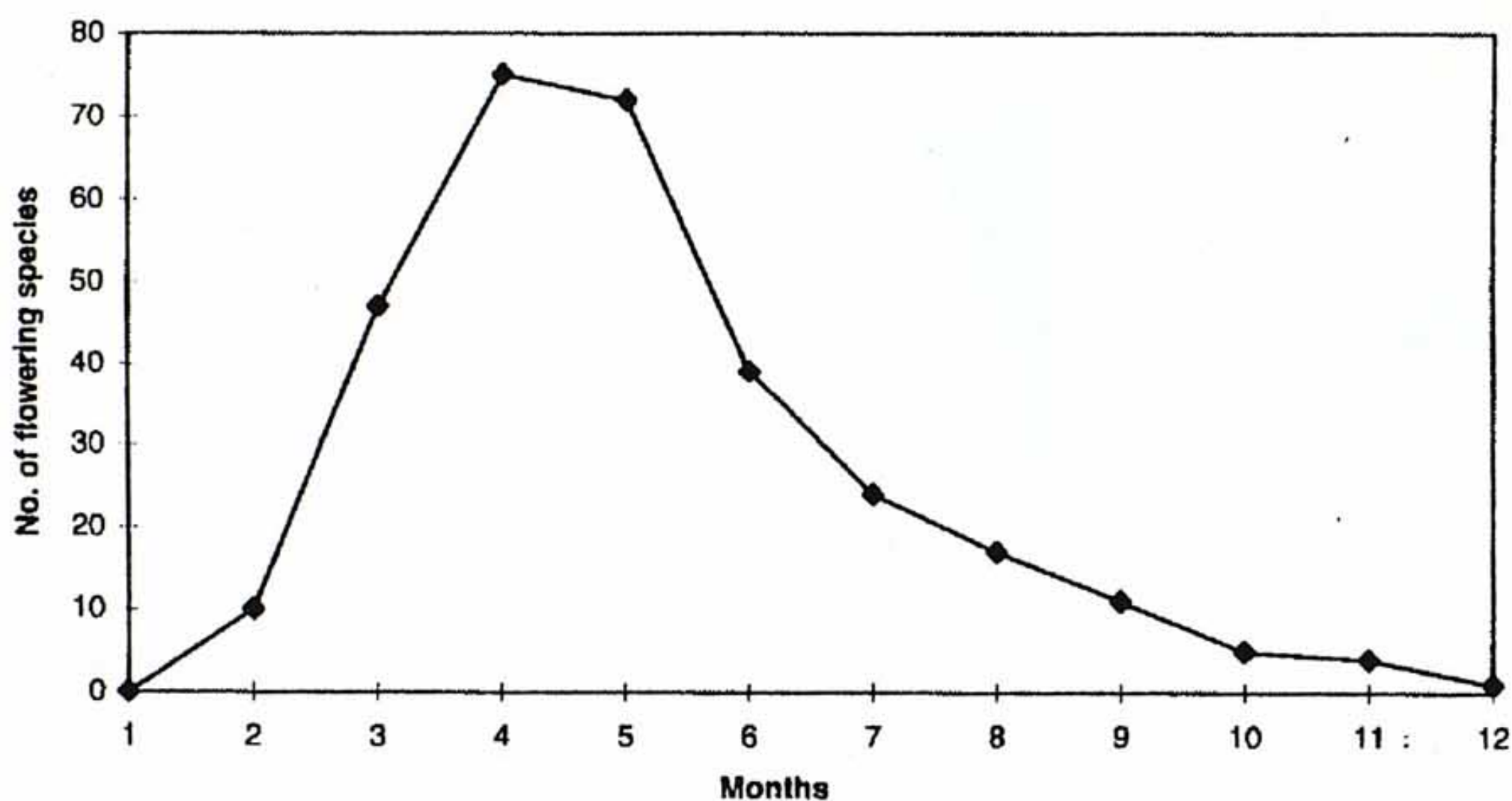


Fig. 2. Annual flowering cycle of Israeli *Apiaceae*.

### Temporal dispersal modes

According to our studies, three principal modes of dispersal rates were recognized, as well as an additional multiple-mode type (Fig. 3):

*Mode 1, prompt.*- All the diaspores are dispersed soon after maturation, in a short period of 45-60 days. Most species accomplish their dispersal in May, with the first dry weeks of spring. The described type (Fig. 3a) was discerned and measured in 6 species (e.g., *Scaligeria napiformis* and *Heptaptera anisoptera*), and recognized in 23% of the studied species.

*Mode 2, gradual.*- The diaspores are dispersed gradually, in a slow rate, from maturation till the end of the dispersal season, in a long time-span of 100-170 days (Fig. 3b). The "gradual" is the most common mode. It was recorded in 10 species in both study sites, and includes 53% of all 94 species. In some species, the range of dispersal time is shortened by a late blooming (e.g., *Ferulago syriaca* and *Pimpinella peregrina*). In other species it is shortened by completing the dispersal of all the seeds long before the new year's rains (e.g., *Scandix pecten-veneris*).

*Mode 3, totally Retarded.*- The diaspores are not discharged from the mother plant during most of the potential dispersal season, and the process is totally retarded till the first rains. In a few species (e.g., *Oenanthe prolifera* and *Eryngium glomeratum*) the fruits remain constantly attached (see above: "Mericarps and diaspores"), whereas in others, the diaspores are practically detached or able to do so, but they do not fall as they are trapped in the infructescence by the peripheral organs (e.g. *Exocantha heterophylla*). Only ten species (11%) have been included in this mode (Fig. 3c).

*Alternative mode multiple.*- This mode features a combination of the above modes. It can be considered as a different mode since it represents a particular ecological strategy (LLOYD, 1984; PLITMANN, 1986). In this type, some of the diaspores are carried



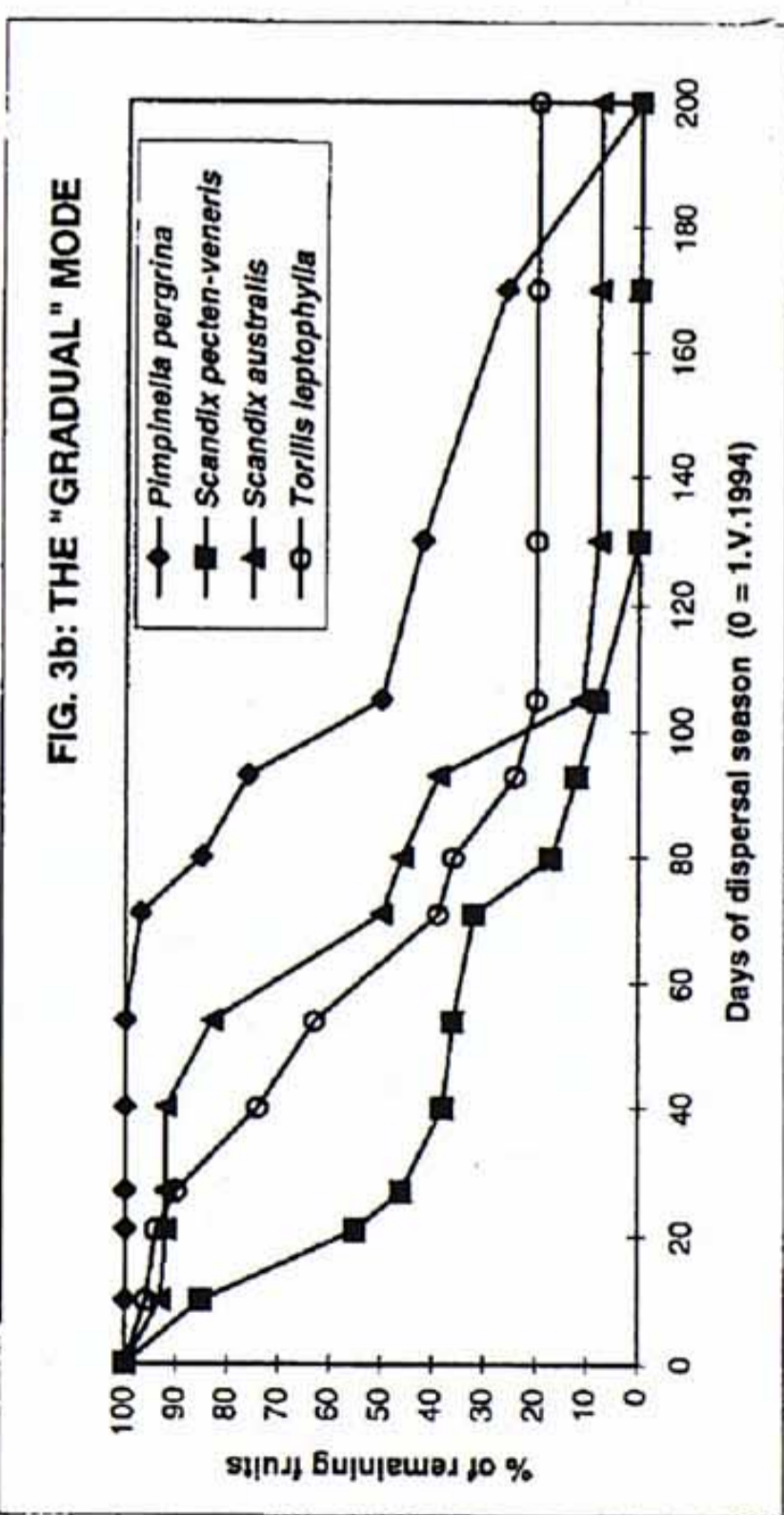
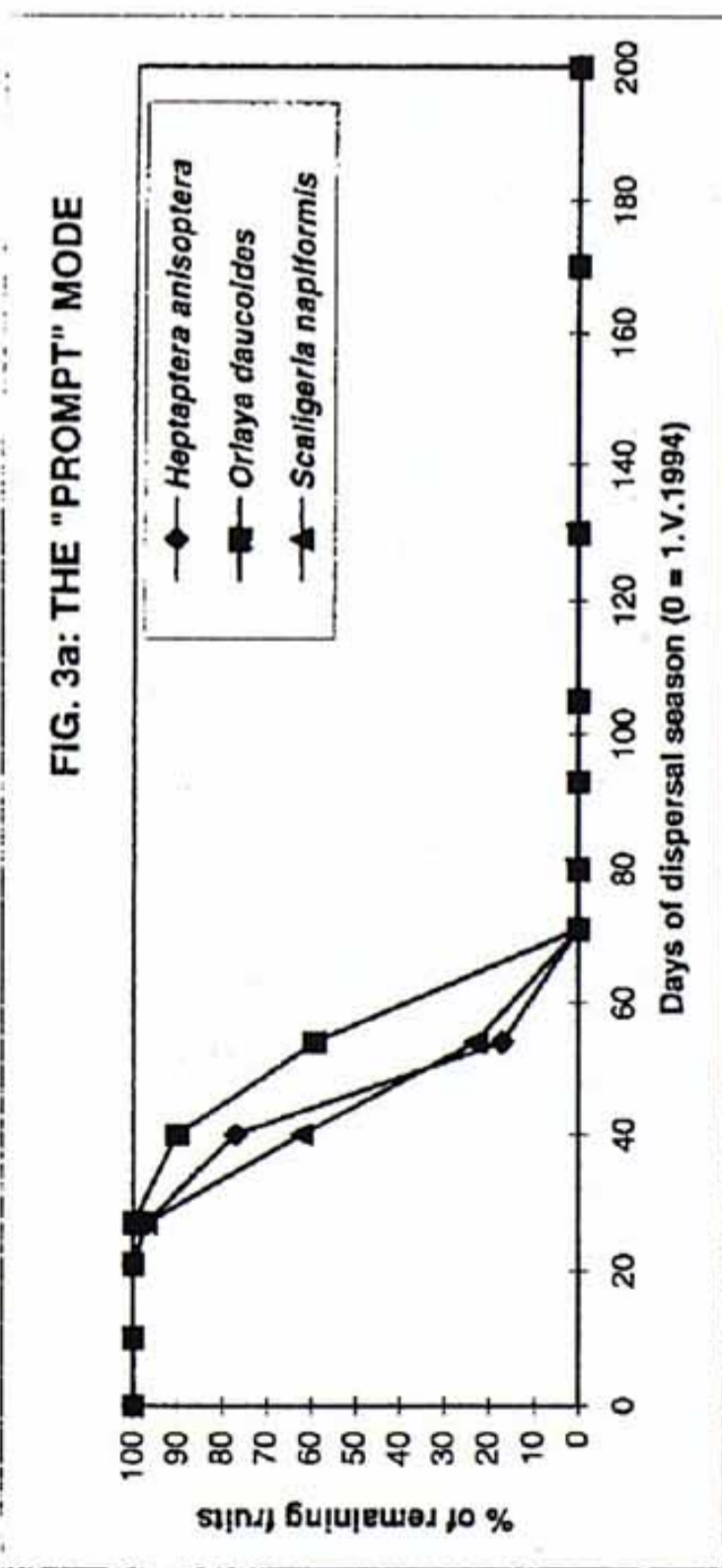
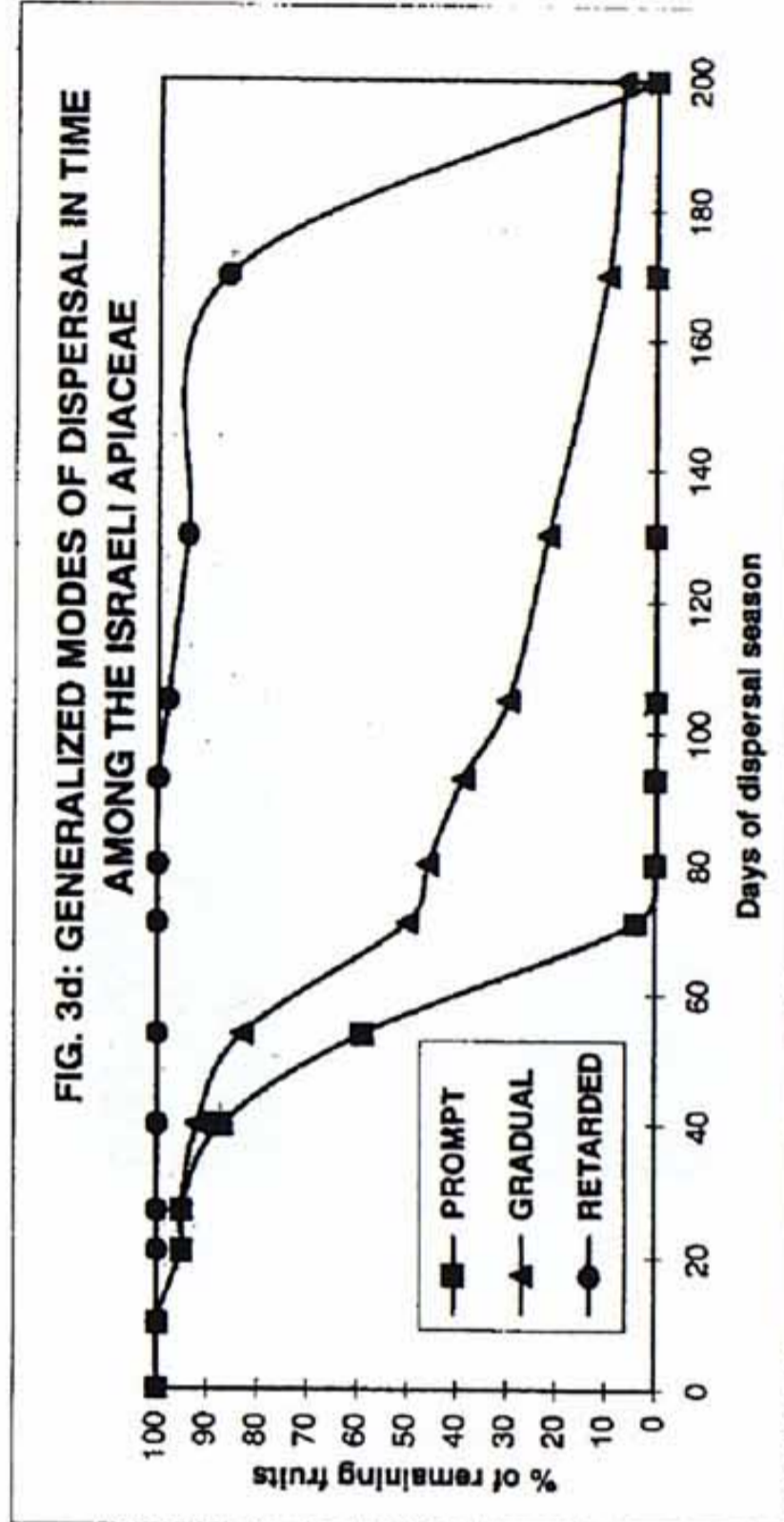
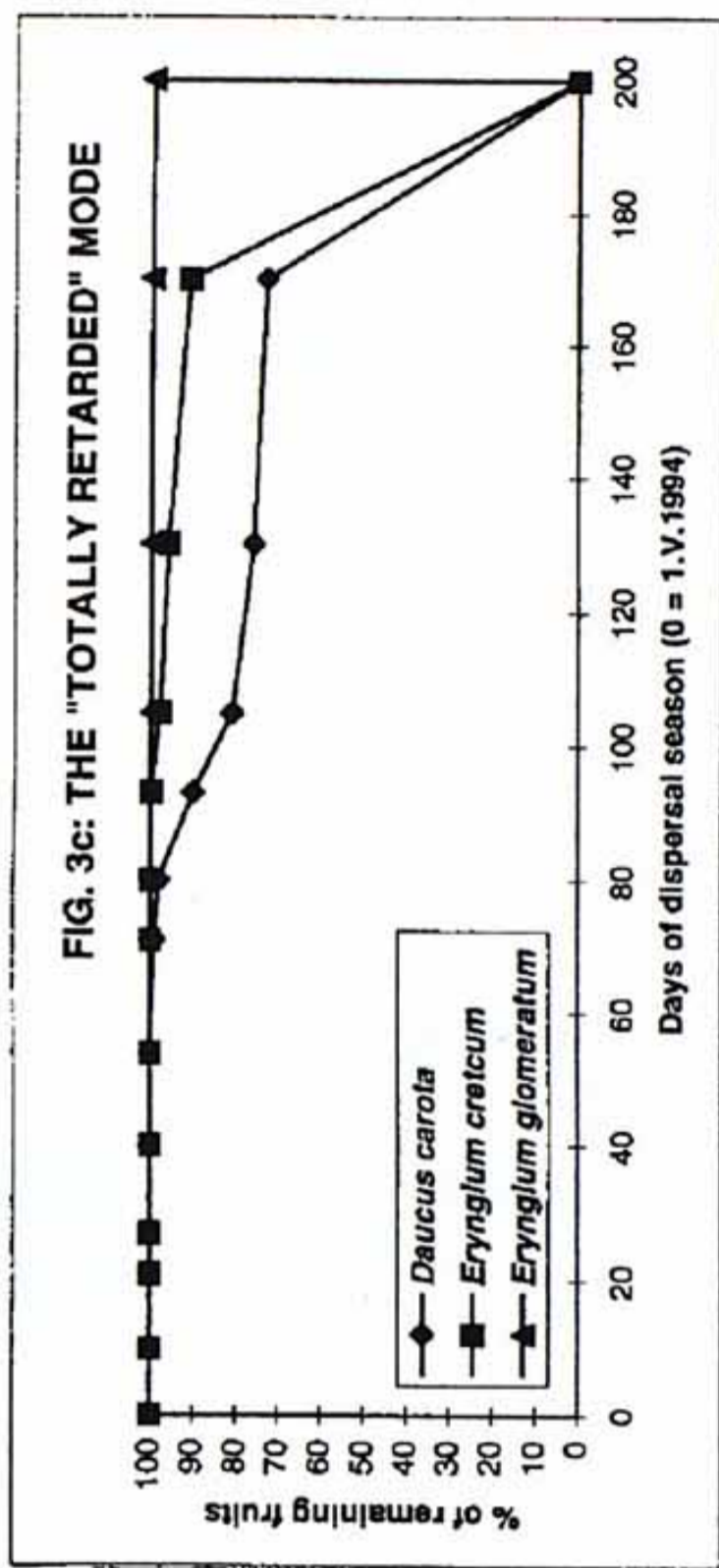


Fig. 3. The principal temporal dispersal modes: 3a, Prompt; 3b, Gradual; 3c, Retarded; 3d, Generalized model. (X axis: 0 = 1.V.1994; 175 = first rain).



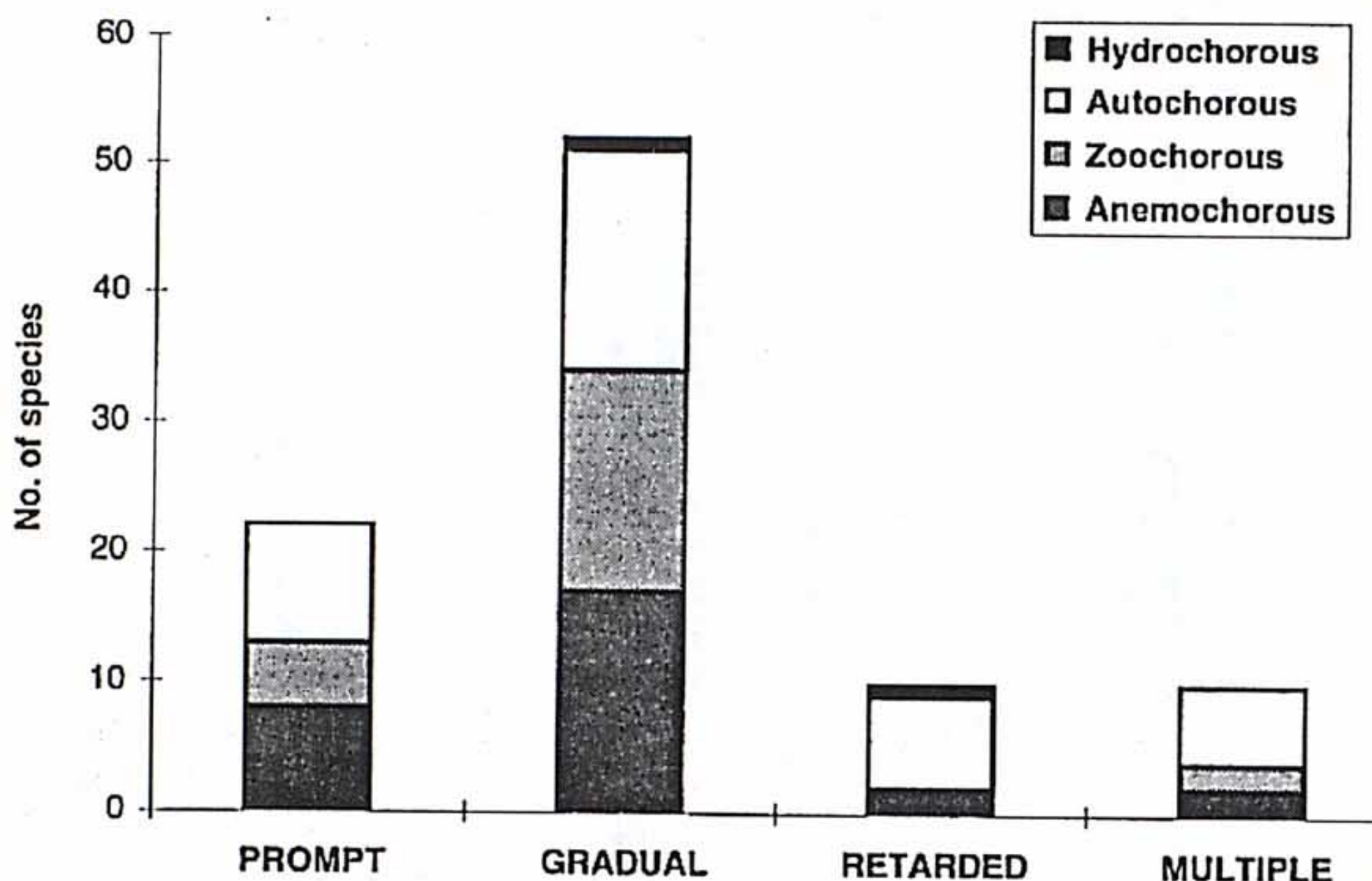


Fig. 4. Spatial types according to temporal dispersal modes.

away, and the remainders are retarded. The characteristic species of this mode are heterocarpic plants (e.g., *Scandix palaestina*, *Torilis leptophylla*), in which the heterocarpy is expressed not only in the difference in the mericarps' shape, but also in their discharged/undischarged function. In other species, only small amounts of diaspores do readily fall, while the major part of them does not, owing to special mechanisms such as hygrochasy (e.g. *Daucus carota*, *Synelcosciadum carmeli*, *Ammi visnaga*). Ten species (11%) feature this mode.

Within the "Gradual" mode, three principal temporal patterns were discerned:

1. *Short-time continuous*.- The diaspore flow is continual and in more or less equal rates, but all the mericarps are carried out long before the potential dispersal season is over. This pattern was recorded for *Scandix pecten-veneris* and was observed in other species (e.g., *Lecokia cretica* and *Bunium paucifolium*).

2. *Bi-sequential ("double-peaked")*.- The diaspore flow occurs in two phases with a time lapse of no dispersal in-between. Two factors were recognized as responsible for this pattern: a difference in carpophore structure (i.e., a difference between the tissues connected to the pedicel), and heterocarpy. In *Torilis tenella* for instance, the tissues of the carpophore's base are unequal - the adaxial is thin and the abaxial is thicker. Therefore the abaxial mericarp falls easily, whereas the upper one remains attached. In some heterocarpic species, the difference in the shape of the mericarps affects the dispersal in time as well as the dispersal in space. In *Scandix australis*, which bears two kinds of mericarps in each umbellet, the outer ones spread out and fall first (within about 90 days after maturation); the inner/central single fruit remains connected to the pedicel and is dispersed after a time-lag, when the stems are broken.



Mode	Number of species	Life			Spatial mode			
		A-B	H-C	An	Zo	Au	Hy	
Prompt	22	18**	4**	5	5	9	8	
Gradual	52	24*	27*	17	17*+	16**	1	
Totally Retarded	10	3*	8*	2	8*	8*	1	
Multiple	10	9*	1*	2	2	6	8	

X<sup>2</sup> test: difference from expected value significant at \*\*) P ≤ 0.01, \*) P ≤ 0.05.

Table 2. Life forms and Spatial dispersal modes (see Table 1 for abbreviations) according to temporal dispersal modes in Israel Apiaceae.

All these modifications of the discharge rate of a species are included in the gradual mode, as no fruits, or only a few, remain at the end of the potential dispersal season. In contrast, heterocarpic species with some kind of fruits which are totally retarded, pertain to the Multiple mode. The bi-sequential pattern is recognized also in the Prompt mode, in *Chaetosciadium trichspermom*, which has two types of mericarps in each fruit.

3. *Perpetual and truncated*.- The diaspores flow is slow and regular during the whole dispersal season. Towards the end of the season (first rains), a small amount of fruit is still undispersed and dissemination (discharge) is seemingly incomplete. This "truncation" was recognized in typical tall species (e.g., *Ferula communis*, *Pimpinella peregrina* and *Conium maculatum*). Most of the remaining diaspores would be dispersed later by the Fall winds.

#### Associations between Temporal modes and Spatial modes or Life forms

Possible associations between the temporal modes and other features are presented in Figures 4-5. Spatial modes are partially associated with the temporal modes (Table 2, Fig. 4). All types of spatial modes are equally distributed among the prompt and multiple temporal modes. Zoochory is significantly more common in the gradual and absent in the totally retarded modes, while autochory is significantly more common in the totally retarded mode, and less common in the gradual mode. Life forms are also associated with the temporal modes (Table 2, Fig. 5). Annuals are significantly more common in the prompt and multiple modes, whereas perennials are more common in the gradual and totally retarded modes.



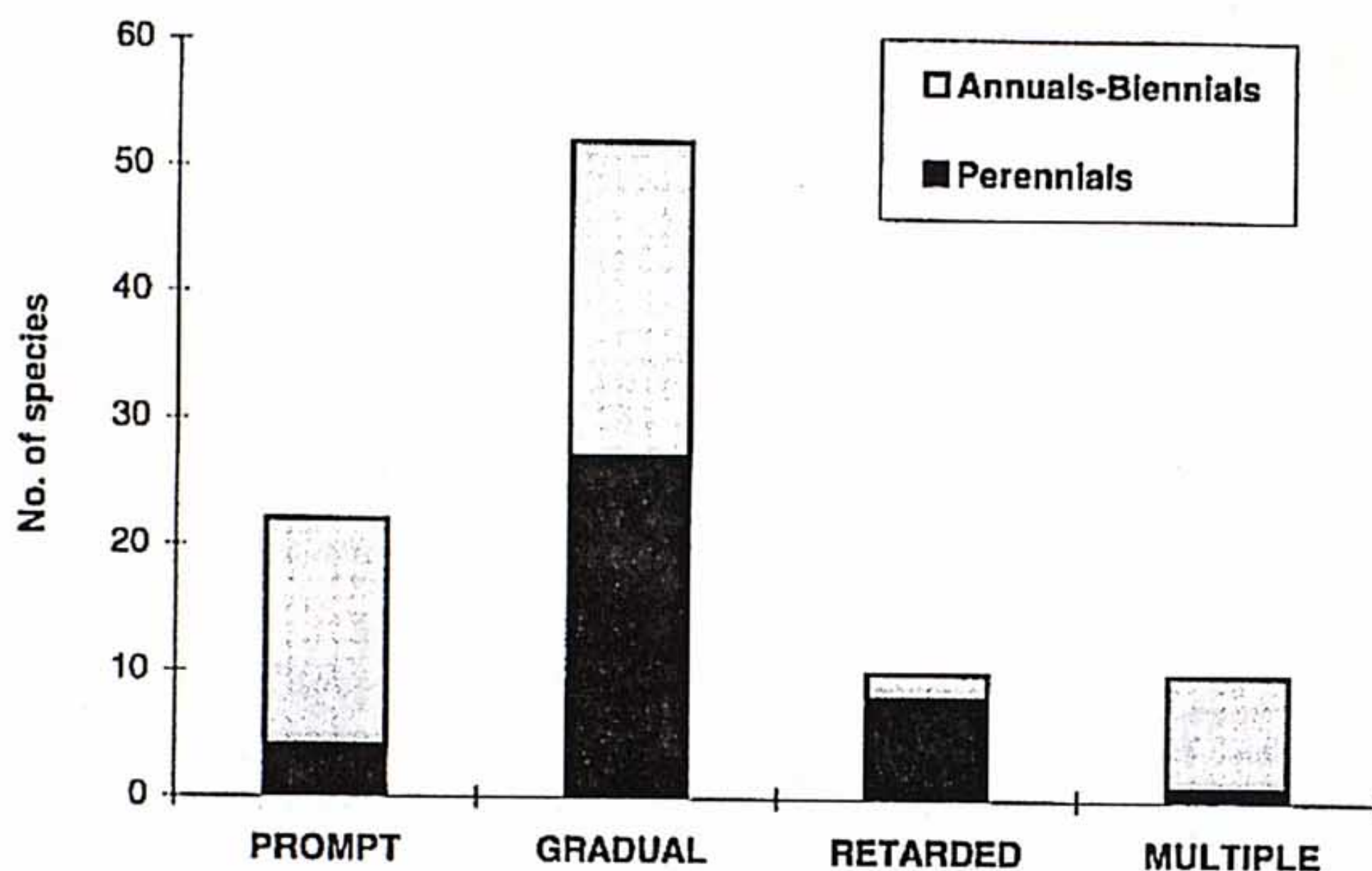


Fig. 5. Life forms according to temporal dispersal modes.

## Discussion and Conclusions

### Spatial dispersal modes

Our studies show (Table 1), that as expected, the morphological-anatomical characters of the Apiaceous fruit (size, shape and structure), more or less correspond with the traditional conception of their spatial dispersal vectors. The most exceptional result is the high percentage (42%) of the autochorous species among the Israeli *Apiaceae*. Several authors (e.g., CERCEAU-LARRIVAL, 1971; STEBBINS, 1971) pointed out that the smooth sphaerical/cylindrical fruit type of the *Apiaceae*, lacking specialized means of dispersal, is usually associated with restricted dispersal distance, hence it is considered a primitive, basic character in this family. However, this "generalist" fruit type is perhaps adapted to other components of the dispersal strategy, i.e. to the temporal factor, and probably to vectors of carry-over of the diaspores. With regards to the time factor, fruit morphology may be of secondary importance and the same fruit types that share a spatial mode of dispersal, may differ in their temporal mode.

The significant association of two spatial modes of dispersal with particular life forms (anemochory with perennials and zoochory with annuals, Table 1) seems to reflect an association between the height of the individual and its mode of dispersal. In Israel, most of the perennial *Apiaceae* are taller than the annuals (COHEN & PLITMANN, unpubl.). Accordingly, we suggest that species that feature anemochory should be taller (mostly perennials), contrary to species featuring zoochory which should be generally lower (mainly annuals). Similar associations of height and dispersal



modes were reported in the vegetation of northern temperate woodlands by HARPER & al. (1970).

#### **Factors that control the temporal modes of dispersal**

The temporal aspects of dispersal behavior of a population can be determined by the timing and duration of the dissemination process (i.e. dates of initiation and termination), and the rate of shedding diaspores. As presented in Figure 2, the typical phenology of each species is a factor that significantly affects the timing of fruit maturation and, in most species (except for those of the totally retarded mode), also the starting time of discharge. For most of the species that begin their dispersal during June-September (25%), the timing and duration of the dispersal is directly derived (i.e. delayed and/or decreased) from the timing of the flowering period (e.g., *Hippomarathrum boissieri*, *Sison exaltatum*, *Deverra tortuosa*). In some cases the timing of the reproductive phase depends upon other factors, not related to dispersal strategies but rather to resources available and environmental conditions. For instance flowering in wet habitats during the summer occurs in accordance with the environmental conditions (e.g., *Foeniculum vulgare*, *Apium graveolens*), or Fall flowering might be related to pollination strategies (e.g., *Ferula biverticillata*).

The main functional external factors that enhance the discharge of the mature/dry diaspores are humidity and air movement, both change according to local niche conditions. According to our observations, all the species of the prompt mode disseminate most of their diaspores during several periods of dry-hot and windy days which are usually common in Israel during May. The species of the totally retarded mode discharge their diaspores during the Fall rain storms in October-November. In contrast, the species of the gradual mode, just begin to discharge a few diaspores with the early summer winds. As pointed out, and checked by us, the internal factor responsible for the delay in the latter two modes is mainly the modification of the carpophore tissue by which the rate of discharge is regulated and the dispersal duration is elongated. In some other cases, different parts of the parental plant are also involved in the delay and/or termination of the dissemination period: fruit pedicel, bracts and bracteoles, abscission stem tissue. The functional factors define the temporal modes. Among the selective forces which directly affect the evolution of the temporal modes, the energy budget (namely, resources available and cost of mechanism) plays a significant role. In this respect, the prompt mode, associated with annuals (Table 2, Fig. 5), is probably the most economical. In the gradual and the totally retarded modes, associated with perennials, energy is invested, in part, in spatial mechanisms, the rest of the effort is spread along the reproductive season.

#### **The role of the temporal factor in dissemination**

The results of our study confirm our initial hypothesis that diverse and well-defined temporal modes of dispersal should exist, corresponding to different strategies. Indeed,



we characterized and quantified such modes (Figs. 3a-c). The described principal temporal modes (Fig. 3d) within the Israeli *Apiaceae*, represent divergent ecological strategies or adaptations, each mode may contribute to the fitness of the species involved, by increasing the rate or efficiency of dispersal and by reducing potential offspring competition.

The prompt mode can be regarded as the simple basic strategy. In the species adopted this mode, the diaspores are discharged immediately after the fruit has dried. A small amount of energy is invested in the dissemination process. The timing of flowering (whether early or late) directly determines the timing of seed-flow. The equal distribution of the spatial categories among the prompt mode (Table 2) is an indication that, in this case, the adaptation to spatial dispersal was the principal factor of diversity.

The gradual mode may represent an evolutionarily advanced mode in which certain mechanisms that delay dissemination could be involved. This delay is usually controlled by the plant's tissues and actually affects the timing and duration of the dispersal. The patterns recognized by us within the gradual mode are partial, referring only to the Israeli *Apiaceae*, and further quantitative studies must be performed before reaching general conclusions. Within this mode, there are significantly more zoochorous species (spiny or hooked mericarps) than autochorous ones (Table 2). We can assume that selection towards passively carrying of diaspores by animals, naturally in slow rates, has been combined with selection of this temporal mode. The gradual mode, in particular, fits the theoretical model of parent-offspring conflict (e.g., MOTRO, 1983), in which the optimal dispersal rate is determined by the parental plant. We can also assume that the high percentage of species adapting this mode among the Israeli *Apiaceae*, indicates that the gradual mode evolved as one of the prevalent dispersal strategies in the Mediterranean ecosystem.

The totally retarded (11% of the species) and the multiple (11%) modes are exceptional and probably represent specific adaptations. The totally retarded mode may be regarded as an optimal strategy, particularly in Mediterranean climate, by using the same vector - Fall rain storms, for both dispersal and germination. The multiple mode is considered as an advanced mode, since some alternative strategies are combined within. The fact that autochorous species are significantly more common and zoochorous species are absent in within this mode (Table 2), might indicate that certain Autochorous species are not really "generalized" and do have specific dispersal behavior, as discussed above.

Several advantages of the temporal modes can be briefly suggested: (1) Adaptation to escape from adverse conditions. The ecological stresses (e.g., extreme temperature, predation) on the parental plant are obviously different, and probably better, than those on the ground. Hence, the diaspores in the prompt mode will have to confront the ground conditions, as well as potential competition, in contrast to the totally retarded ones which endure only the milieu of the parental plant. The diaspores in the gradual mode persist between both ground and parental environments. (2) Spreading the risk of seed mortality and increasing their chances of survival may also account for the differences between the modes. The species of the gradual mode spread the risk/chance in time, in contrast to the other modes. (3) Likewise, timing of dispersal on a particular date when the conditions are optimal, increases the effectiveness of dispersal.



Adaptation to specific period of time may be related to the prompt, totally retarded or multiple modes, when most of the seeds flow in a short time-span.

As indicated, when the spatial type is less functional (as in autochoty), the temporal mode is more significant in the adaptive strategy. Yet, from the associations between specific temporal and spatial modes we can infer that in some cases both aspects participate in the dispersal strategy of a particular species. We can conclude that, in parallel to the well-known spatial modes, plants feature diverse temporal strategies and the temporal factor in dispersal is just as important as the spatial one.

## Appendix 1.

**The Apiaceae species in Israel (excluding extinct, confused and cultivated species).**

**\*) species measured and examined at the study sites.**

- |   |   |
|---|---|
| <i>Ainsworthia cordata</i> Boiss.               | <i>Deverra triradiata</i> Hochst.               |
| * <i>Ainsworthia trachycarpa</i> Boiss.         | <i>Eryngium barrelieri</i> Boiss.               |
| <i>Anthriscus lampocarpa</i> Boiss.             | * <i>Eryngium creticum</i> Lam.                 |
| <i>Ammi majus</i> L.                            | <i>Eryngium falcatum</i> F. Delaroche           |
| <i>Ammi visnaga</i> (L.) Lam.                   | * <i>Eryngium glomeratum</i> Lam.               |
| <i>Apium graveolens</i> L.                      | <i>Eryngium maritimum</i> L.                    |
| <i>Apium nodiflorum</i> (L.) Lag.               | <i>Exoacantha heterophylla</i> Labill.          |
| <i>Artedia squamata</i> L.                      | <i>Falcaria vulgaris</i> Bernh.                 |
| <i>Astoma seselifolium</i> DC.                  | <i>Ferula biverticillata</i> Thieb.             |
| <i>Bifora testiculata</i> (L.) Schultes         | * <i>Ferula communis</i> L.                     |
| <i>Bunium ferulaceum</i> Sm.                    | * <i>Ferula daninii</i> Zohary                  |
| <i>Bunium paucifolium</i> DC.                   | <i>Ferula meironensis</i> sp. nov.              |
| <i>Bupleurum brevicaule</i> Schlecht.           | <i>Ferula negevensis</i> Zohary                 |
| <i>Bupleurum gerardii</i> All.                  | <i>Ferula orientalis</i> L.                     |
| <i>Bupleurum lancifolium</i> Hornem.            | <i>Ferula sinaica</i> Boiss.                    |
| <i>Bupleurum libanoticum</i> Boiss. & Bl.       | <i>Ferula tingitana</i> L.                      |
| <i>Bupleurum nodiflorum</i> Sm.                 | * <i>Ferulago syriaca</i> Boiss.                |
| <i>Bupleurum odontites</i> L.                   | <i>Foeniculum vulgare</i> Miller                |
| <i>Bupleurum orientale</i> Snogerup             | * <i>Heptaptera aniosoptera</i> (DC.) Tutin     |
| <i>Bupleurum semicompositum</i> L.              | <i>Hippomarathrum boissieri</i> Reut. & Husskn. |
| <i>Capnophyllum peregrinum</i> (L.) Lag.        | <i>Hydrocotyle ranunculoides</i> L. fil.        |
| <i>Chaetosciadium trichospermum</i> (L.) Boiss. | <i>Lecokia cretica</i> (Lam.) DC.               |
| * <i>Conium maculatum</i> L.                    | * <i>Lagoecia cuminoides</i> L.                 |
| <i>Coriandrum sativum</i> L.                    | <i>Lisaea strigosa</i> (Banks & Sol.) Eig       |
| <i>Crithmum maritimum</i> L.                    | <i>Malabaila secacul</i> (Banks & Sol.) Boiss.  |
| <i>Daucus aureus</i> Desf.                      | <i>Myrrhoides nodosa</i> (L.) Cannon            |
| * <i>Daucus bicolor</i> Sm.                     | <i>Oenanthe fistulosa</i> L.                    |
| * <i>Daucus carota</i> L.                       | <i>Oenanthe pimpinelloides</i> L.               |
| <i>Daucus guttatus</i> Sm.                      | <i>Oenanthe prolifera</i> L.                    |
| <i>Daucus jordanicus</i> Post                   | <i>Oenanthe silaifolia</i> MB.                  |
| <i>Daucus litoralis</i> Sm.                     | * <i>Orlaya daucoides</i> (L.) Greuter          |
| <i>Daucus subsessilis</i> Boiss.                | <i>Peucedanum junceum</i> (Boiss.) Mouterde     |
| <i>Deverra tortuosa</i> (Desf.) Benth. & Hook.  | <i>Pimpinella corymbosa</i> Boiss.              |



- \* *Pimpinella cretica* Poir.  
*Pimpinella eriocarpa* Banks & Sol.  
 \* *Pimpinella peregrina* L.  
*Prangos ferulacea* (L.) Lindley  
*Pseudorlaya pumila* (L.) Grande  
*Ridolfia segetum* (L.) Moris  
*Scaligeria hermonis* Post  
 \* *Scaligeria napiformis* (Sprengel) Grande  
 \* *Scandix australis* L.  
*Scandix cioliocarpa* O. Cohen  
*Scandix palaestina* Boiss.  
 \* *Scandix pecten-veneris* L.  
*Scandix stellata* Banks & Sol.  
*Scandix verna* O. Cohen
- Sison exaltatum* Boiss.  
*Smyrniium connatum* Kotschy  
*Smyrniium olusatrum* L.  
 \* *Synelcosciadium carmeli* (Labill.) Boiss.  
*Tordylium aegyptiacum* (L.) Lam.  
*Tordylium syriacum* L.  
*Torilis arvensis* (Huds.) Link  
*Torilis gaillardotii* (Boiss.) Drude  
 \* *Torilis leptophylla* (L.) Reichenb.  
*Torilis nodosa* (L.) Gaertner  
 \* *Torilis tenella* (Delile) Reichenb.  
*Torilis webbii* S.L. Jury  
*Turgenia latifolia* (L.) Hoffm.  
*Zosima absinthiifolia* (Vent.) Lin

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