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Anthecology of *Euphorbia*—preliminary studies

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SUMMARY

The floral biology of perennial herbaceous to suffruticose species of *Euphorbia* was studied in various parts of Europe. The extensive range of visitors indicate a lack of specialization from the side of these plants, but apparently there is a dependence of certain solitary bees of spurge as a food plant. Experiments in which flowering branches were enclosed in gauze or nets indicated a strong dependence on entomophily. Self-compatibility is presumably of little incidence, which means that geitonogamy is possible and presumably common. The possible role of non-flying visitors (ants and spiders) is discussed. Some views regarding the anthecology of other *Euphorbia* species and other (and less advanced) genera of the Euphorbiaceae are expressed.

Key-words: Euphorbia, spurge, entomophily, pollination ecology, geitonogamy.

INTRODUCTION

The anthecology of the genus *Euphorbia* has been studied very little (Ehrenfeld 1976; 1979) and a pertaining study was deemed worthwhile. A broad investigation was started by Vroege, but his untimely death rendered further studies impossible for the time being. Additional records by the two other authors (and some experiments by Vinkenoog) yielded sufficient data to draw some preliminary conclusions (Vroege *et al.* 1987).

It must be mentioned that there are scattered and incidental relevant records in entomological and ecological papers (e.g. Kratochwill 1984) but they relate to visiting alone (and usually only to solitary bees as visitors) and do not change the picture obtained from our studies.

LOCATIONS AND METHODS

The following species were studied: *Euphorbia esula* L., at sites in Castricum, Den Helder and Huizen (Province of North Holland, The Netherlands) and the Reichswald (FRG, near Kleve) and cultivated plants in gardens at Den Helder and Huizen; *E. palustris* L. mainly at De Weerribben (Province of Overijssel, The Netherlands); *E. cyparissias* L. (The Netherlands, various places), and occasionally *E. brittengeri* Opiz ex Samp., a population near Cahors, SW France.

A few insects caught on *Euphorbia* were examined by means of SEM. The *Euphorbia* pollen appears to become easily attached to the visitors (examples in Vroege *et al.* 1987). A

This paper is dedicated to Professor Dr T. van der Hammen on the occasion of his 65th birthday.

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Table 1. Insect visitors recorded from *Euphorbia esula* (railway siding near Castricum Station, The Netherlands, July 1984)

Coleoptera		Cantharidae	
		Malachidae	
Lepidoptera		Satyridae	*Pyronia tithonus* (L.)
		Lycaenidae	*Polyommatus icarus* (Rottenb.)*
Hymenoptera		Ichneumonidae	
		Sphecidae	(probably 2 species)
		Apidae	*Apis mellifera* L.
Diptera	Homoeodactyla	Stratiomyidae	*Chloromyia formosa* (Scop.)
	Cyclorrhapha	Syrphidae	*Chrysotoxum bicinctum* (L.)
			Episyrphus balteatus (De G.)
			Eristalis arbustorum (L.)
			E. nemorum (L.)
			E. tenax (L.)
			Helophilus hybridus Loew
			H. trivittatus F.
			Sphaerophoria scripta L.
			Syritta pipiens (L.)
		Muscidae	3 species
		Sarcophagidae	*Sarcophaga* sp.
		Scatophagidae	*Scatophaga stercoraria* (L.)
		Calliphoridae	*Lucilia* sp.
		Tachinidae	2 species
		Sciaridae (= Mycetophilidae)	

*Almost certainly this species (because it is the commonest there and other blues are very rare in the area; the specimen was observed but not caught).

number of insects caught on *Euphorbia* were studied under a binocular microscope and the number of attached *Euphorbia* pollen was counted so as to obtain some idea of the efficacy of the visitors as vectors.

Experiments aimed at assessing the dependence of the species on insect pollination consisted of caging-in flowering branches of a specimen with cyathia before female anthesis, exposed equivalent branches of the same plant acting as controls. Rather coarse-meshed (6 × 8 mm) netting was usually used, but in attempts to prevent ants from entering also a very fine-meshed (0·5 × 0·5 mm) gauze was used. After 5–6 weeks the number of developed fruits on the caged-in branches and control branches was recorded, the developing of fruits being taken as a measure of successful pollinations.

The bulk of the insects caught on *Euphorbia* is represented in the collections of the Entomological Department, Zoological Museum, Amsterdam, a part (only Hymenoptera) is in the private collection of Dr H. Wiering (Bergen, The Netherlands).

RECORDS OF VISITORS

The visitors, partly as the species and partly mentioned as a group, are shown in Tables 1–4. We assume that the animals caught—the spiders excepted—were foraging on the pollen or on the nectar provided by the plant (or on both) as far as can be reasonably ascertained; in

Table 2. Insect visitors recorded from *Euphorbia esula* (Reichswald, Nordrhein-Westfalen, FRG, June–July, 1984)

Coleoptera		Cerambycidae	*Rhagium mordax* De G.
			Judolia cerambyciformis (Schr.)
			Strangalia maculata (Poda)
			S. melanura (L.)
			S. nigra (L.)
		Mordellidae	1 species
		Malachidae	1 species
Lepidoptera		Pyralidae	Crambinae (1 species)
Hemiptera			1 species
Hymenoptera		Apoidea	*Bombus* sp.
			Psythyrus sylvestris Lepel.
		Sphecoidea–Pompilidae	1 species
		Formicoideae	1 species
		Proctotrupoidea	1 species
		Tenthredinae	2 species
		Ichneumonidae	3 species
		Cephidae	1 species
Diptera	Homoeodactyla	Stratiomyidae	*Chloromyia formosa* (Scop.)
		Empididae	1 species
	Cyclorrhapha	Syrphidae	*Cheilosia variabilis* Panz.
			Chrysogaster solstitialis Fallén
			Chrysotoxum bicinctum (L.) var. *tricinctum* Rond.
			Epistrophe ochrostoma Zett.
			Episyrphus balteatus (De G.)
			Eristalis arbustorum (L.)
			E. horticola (De G.)
			E. intricarius (L.)
			E. nemorum (L.)
			E. pertinax (Scop.)
			E. tenax (L.)
			Helophilus pendulus (L.)
			H. trivittatus F.
			Melanostoma mellinum (L.)
			M. scalare (F.)
			Myathropa florea (L.)
			Platycheirus scutatus (Meig.)
			Syritta pipiens (L.)
			Tropidia scita (M. Harris)
			Volucella pellucens (L.)
			Xylotomima nemorum (F.)
		Muscidae	3 species
		Sarcophagidae	1 species
		Scatophagidae	*Scatophaga idea*
			Scatophaga sp. L.
		Calliphoridae	*Lucilia* sp.
		Anthomyidae	1 species
		Conopidae	*Conops flavipes* L.

Table 3. Insect visitors recorded from *Euphorbia palustris* (De Weerribben, NW Overijssel, The Netherlands, June 1984, June 1985)

Coleoptera			
Lepidoptera			
Hymenoptera		Ichneumonidae	3 species
		Tenthedrinidae	3 species
		Argidae	
		Cephidae	
		Chalcidoidea	
		Eumenidae	*Ancistrocerus* sp.
		Apidae species (probably *Halictus*)	
Diptera	Cyclorrhapha	Syrphidae	*Anasimya lineata* (Meig.)
			Cheilosia sp.
			Chrysogaster hirtella Loew
			Epistrophe eligans M. Harris
			Eristalis anthophorinus Fallén
			E. arbustorum (L.)
			E. horticola (De G.)
			E. intricarius (L.)
			E. tenax (L.)
			Helophilus pendulus (L.)
			Lejogaster splendida (Meig.)
			Melanostoma mellinum (L.)
			M. scalare (F.)
			Neoascia dispar (Meig.)
			N. podagrica (F.)
			Parhelophilus versicolor (F.)
			Pipiza bimaculata Meig.
			Platycheirus scutatus (Meig.)
			Syrphus ribesi L.
			Tropidia scita (M. Harris)

the case of bees the presence of pollen grains on the corbiculae (or in large quantities on the body) was considered an indication of pollen gathering. The lists are by no means exhaustive; there are unlisted records by Vroege and by Meeuse of visitors, mainly on *Euphorbia cyparissias* and *E. paralias*: Neuroptera–Chrysopidae, various species of *Bombus* and Sphegidae (*Oxybelus*, cf. *Cercis*, cf. *Crabro*) and numerous flies (e.g. Anthomyidae), Hemiptera and Dictyoptera.

If the results are assessed above the species level, the following conclusions can be drawn from the records.

(1) The overall visitor spectrum does not differ appreciably between species or localities and not essentially from American records published by Ehrenfeld (1976; 1979). The range of visitors and their total numbers are considerable and as most of them carry pollen on their bodies, and some species even appreciable numbers of grains, one may conclude that as a rule, and under not too adverse climatic conditions, together the visitors accomplish a maximum number of pollinations. Indeed, in normal years the rate of fruit set appears to be very high in the species studied.

Table 4. Insect visitors of *E. brittingeri*. Lot, Le Montat, France, 14–19 May 1986 (Det. H. Wiering)

Hymenoptera		
Sapigydae	*Sapyga quinquepunctata* F.	1 female
Chrysidae	*Chrysis rufiventris* Dhlb.	3
	C. refulgens Spin.	2
Vespidae	*Sulcopolistes semenowii* Mor.	1 female
	Eumenes pedunculatus Pz.	1 male
Apidae	*Nomada sheppardana* K.	1 female
	Andrena combinata Christ	1 female/3 male
	A. chrysosceles K.	3 female
	A. subopaca Nyl.	1 female
	Halictus politus Schck.	16 female
	H. glubriusculus Mor.	7 female
	H. pauxillus Schck.	2 female
	H. kessleri Brams.	1 female
	H. smaragdulus Vach.	1 female

Additional records include numerous flies (of the same groups as recorded in the Netherlands), thomisid spiders (*Misumena* and other taxa) and small anthophilous beetles.

(2) Some visitors appear to be only casuals (e.g. the Lepidoptera) and other ones too rare to contribute much to the total number of pollinations. The most frequently encountered taxa belong to the Diptera and the Hymenoptera, but, depending on the locality and the habitat, different genera and species may dominate; the syrphid *Volucella pellucens* and cerambycid beetles were frequently observed feeding on *E. esula* in the Reichswald, but since these insect taxa do not, or rarely, occur in the western Netherlands they were not recorded as pollinators in our Dutch localities. In the marshy habitat preferred by *E. palustris* quite a few visitors were also wetland species (e.g. Stratiomyidae, some syrphids such as *Helophilus* spp., *Parhelophilus* and *Anasimya*). In France, species were caught that presumably do not, or infrequently, occur in the Netherlands (and vice versa). As stated before, our lists all show the same aspecific pattern in spite of the different localities and circumstances.

It is to be expected that a seasonal change in the insect fauna will be reflected in the lists of visitors, some early species dying off and other ones appearing on the scene later, but this will not result in a different rate of successful pollinations. The principal groups of visitors (Diptera and Hymenoptera) are sufficiently represented by a number of species throughout the flowering season of the species studied.

POSSIBLE EFFICACY OF VISITORS AS POLLEN VECTORS

In view of the fact that each cyathium contains only three ovules, even frequent insect visitors carrying only a few pollen grains may well contribute substantially towards a maximum number of pollinations. Visitors crawling around on the inflorescences

Table 5. Number of pollen grains of *Euphorbia* present on insects caught on *E. palustris* (De Weerribben)

Coleoptera	*Cantharis* sp. (common visitor)	15
	Mordellidae sp. (common, permanent visitor)	10
Lepidoptera	Incurvariidae, 1 species	6
Hymenoptera	*Tenthredo solitaria* Scop.	180
	Apidae sp.	538
Diptera	*Calliphora* species	475
	Eristalis anthophorinus Fallén	50
	Helophilus pendulus (L.)	70
	Melanostoma scalare (F.)	22
	Muscidae (average of 2 species)	18
	Neoascia podagrica (F.)	16
	Odontomyia tigrina (F.)	246
	Parhelophilus versicolor (F.)	31
	Sarcophaga sp.	24
	Scatophaga lutaria (L.)	18
	Tropidia scita (M. Harris)	78

Table 6. Number of pollen grains of *Euphorbia* present on insects caught on *E. esula* (Reichswald)

Coleoptera	*Strangalia maculata* (Podw)	60
Lepidoptera	Unidentified microlepidopteron	6
Hymenoptera	Ichneumonidae (2 large species)	100
	Ichneumonidae (1 small species)	30
	Tenthredo solitaria Scop.	113
	Lasius cf. *Lasius brunneus* (Latr.)	4
Diptera	*Eristalis nemorum* (L.)	100
	Helophilus pendulus (L.)	45
	Melanostoma mellinum (L.)	12
	Scatophaga stercoraria (L.)	68
	Syritta pipiens (L.)	12
	Volucella pellucens (L.)	32

(e.g. many flies, Tenthredinae, beetles, pollen-gathering bees) may effect a large-scale geitonogamy.

Tables 5 and 6 show that most visitors carried at least some pollen grains and the total output as pollinators may be high. It also follows that if mostly geitonogamous pollinations result, the question of self-incompatibility is a very relevant one. We studied this point only tentatively. Attempts to carry out artificial selfing were rendered unreliable owing to the presence of the ubiquitous garden ants that could dip through and spoil the experiment. We do not expect that self-incompatibility occurs in the species studied simply because

Table 7. Rate of seed set in encased plants and in exposed controls

	E. palustris (1985)		*E. esula* (1984)	
	Encased	Exposed	Encased	Exposed
Plants used in experiment (*n*)	5	17	5	10
Mean number of fruits/cyathium	17	72	14	24
Number of seeds per fruit (% of total)				
With 0 fruit	49 (59)	0 (0)	45 (63)	68 (28)
1 fruit	12 (15)	13 (1)	1 (1)	2 (1)
2 fruits	9 (11)	119 (10)	8 (11)	36 (15)
3 fruits	13 (16)	1088 (89)	18 (25)	135 (56)
Total number of cyathia*	83	1220	72	241
Total number of seeds formed	69	3515	71	732
Rate of seed set (%)	28	96	33	65

	Encased	Exposed
Number of fruits containing seeds		
With 1 seed	2	69
2 seeds	—	19
3 seeds	—	25
Total number of cyathia*	338	356

*Number of withered ones without seed-set. The weather conditions were very inclement at the time.

geitonogamy must occur much more frequently than outbreeding. Another indication is that small, isolated stands of several of the *Euphorbia* species (*E. cyparissias* and *E. palustris*) are in fact clones as a result of the formation of underground runners developing into daughter individuals. As far as could be ascertained such isolated patches produced appreciable quantities of fruits, but no serious attempts were made to elucidate this matter further.

DEPENDENCE ON ENTOMOPHILY

The results of an exclusion of insect visitors by caging parts of plants were unfortunately not satisfactorily consistent (Table 7). Sometimes the screening-off totally prevented seed set, but in other cases some fruits developed. Sources of error were: the difficulty of keeping the screening gauzes or netting far enough away from the inflorescences (when they touched an inflorescence insects had access to the cyathia through the screen), pollinations by ants, thrips or spiders inadvertently enclosed, and possibly the effects of strong gusts of wind or rain. The adhesive properties of the pollen grains are presumably prohibitive to their easily becoming air-borne. We expect that to all intents at least spurges of the type studied depend entirely on animal pollen vectors for their reproduction.

DISCUSSION

Generalities

Our studies suggest that the *Euphorbia* species studied are visited by a wide range of insect visitors, most of which have a palynophilous pubescence. These visits must result in an appreciable number of (mainly geitonogamous) pollinations of the protogynous cyathia. Self-compatibility, therefore, seems to be a pre-requisite for adequate seed-set.

We feel that our findings may be generalized and that most species of *Euphorbia*, including the numerous African succulent and leafless ones, exhibit the same pollination syndrome. However, one must expect that some species are more specialized and attract fewer species—the ornithophilous poinsettia is an extreme and aberrant case because it attracts only humming birds and certain butterflies. Species with a brief flowering time may be specialized because only insects active at that time come to visit and act as pollen vectors. The role of toxic substances has been mentioned and deemed insignificant in most cases (see above).

From a phylogenetic point of view one may consider the alternatives of a primacy of anemophily or of ambophily/entomophily in the primarily and nowadays almost consistently diclinous family Euphorbiaceae. Entomophily in diclinous taxa is not at all rare and several diclinous ones are ambophilous (Salicaceae for instance).

One must not underrate the attractiveness of euphorbiaceous inflorescences to insects. Many have semaphylls of a kind, or white to yellow inflorescences, and using the well-known indoor ornamental *Codiaeum variegatum* as an example, produce an attractive scent and copious nectar. Optical and olfactorial attraction clearly play a part and we believe that ambophily or even zoophily was the original pollination syndrome in the family. *Euphorbia* and some related genera are specialized because their pseudanthial blossoms act as monoecious (and protogynous) ones, whereas in most other cases (the Phyllantheae excepted) the sexual organs are spatially separated, which favours out-breeding especially in dioecious genera. Conceivably wind-pollination prevailed in the progenitors of the Euphorbiaceae, but we think ambophily must have originated early. Daumann (1972) came to the conclusion that *Mercurialis* is secondarily anemophilous. We agree that the small, herbaceous and manifestly advanced European species of this genus (advanced in respect of the usually arborescent tropical genera) may be anemophilous, but believe it to be descended from ambophilous (and diclinous) ancestors.

Whether the evolutionary speculations have any bearing on the classification of the family remains to be seen. The anthecology of the numerous tropical taxa is virtually unknown and should be thoroughly investigated.

Qualities and properties of pollen and nectar

The vegetative parts of *Euphorbia*, especially the latex, are suspect from a toxicological point of view. Vague and unconfirmed newspaper reports of insects (or their larvae) and humans suffering ill effects after consuming nectar or honey contaminated by *Euphorbia* pollen seem to be unfounded judging by our own records of pollen consumption of quite a number of visitors (e.g. Neuroptera, beetles, some syrphids) and the specialization of the monolectic solitary bees that collect pollen for their brood. It does not follow that none of the species of the large genus *Euphorbia* has poisonous pollen; conceivably it may be a cause of specialization restricting the visitor spectrum to poison-resistent or purely nectar-consuming insect species. Such speculations can only be substantiated by a study of as many diverse species of *Euphorbia* as possible, but it is more than likely that in view of the prevalence of entomophily the pollen of most species is not toxic to visitors on which the plants depend for their sexual reproduction.

The nectar is, in the species we studied at least, not offered in the form of drops but is present as a thin layer over the nectariferous involucral bracts from which no liquid can be extracted by means of fine glass capillaries (for obvious reasons the ornithophilous poinsettias produce large quantities of liquid nectar, but this must by an exceptional case). In spite of this condition many Hymenoptera with a sucking proboscis (solitary andreniid, halictid and megachilid bees in particular) are frequent, and some even monolectic, visitors. Most nectar-consuming flies will have no problems feeding on the nectar.

The nutritional value of the nectar and its quantity must be high judging by the popularity of the spurges as foraging plants even in stands with rather similar blooms (Compositae, Umbelliferae, *Valeriana*, Dipsacaceae, etc.). We could not devise a suitable method to extract nectar for sugar analysis and recommend further investigation. It is not clear how Percival (1985) obtained her analytical data (which only refer to the sugars and not to other nutrients).

The possible role of ants and spiders as pollinators

Many species of ants are frequent visitors of nectar-producing plants and they have been mentioned as prospective pollinators of some of the plants they visit regularly. In quite a number of cases the ants have access to the nectar without coming into contact with the anthers, but in other cases (as in *Euphorbia*) they may crawl over the genitalia. Indeed we found pollen grains of *Euphorbia esula* on *Lasius brunneus* caught on that spurge, and observed pollen grains of an unidentified exotic *Euphorbia* on workers of *Lasius niger* that had been foraging on that plant in the hothouse. Ants, especially *Lasius niger*, were frequently seen on *Euphorbia* in such quantities that they may well act as pollinators. Fowler (1983) recorded frequent visiting of *Euphorbia esula* by the ant *Formica palledifulva* and (by marking worker ants) sometimes a fidelity to the spurge, but he did not study the possible anthecological consequences. Hagerup (1943) found that in the very hot desert south of Timbuktu (Sahara) anthophilous insects were scarce, ants excepted, and concluded that they acted as pollinators of *Euphorbia granulata, E. scordifolia* and *Phyllanthus 'niruri'* because there was copious fruit-set. In Denmark he found ants almost exclusively as visitors of the small spurges *E. exigua, E. helioscopa* and *E. peplus*. Without ants or other insects no fruits developed and he concluded that ants are the usual pollinators.

In view of the possible toxic effects of ants on the pollen grains they carry on their body and the small amount of grains an ant carries at the same time (about four, possibly the result of intensive preening), only carefully planned experiments in which only ants are permitted to visit *Euphorbia* plants may decide the issue.

The possible pollination by thomisid spiders has been reported elsewhere (Vroege *et al.* 1987). Spiders may carry more than 100 pollen grains, partly removed from the bodies of their prey (because a part of this pollen load is of extraneous origin) and partly hailing from the inflorescence acting as their hiding place. Theoretically at least both cross-pollination and geitonogamy may be achieved when the spider jumps about when catching a prey, but this still needs experimental confirmation.

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