human *Blym*-1 was compared to the amino-terminal regions of both the amino- and carboxyl-terminal halves of human transferrin, ovotransferrin, and lactoferrin (*12*) and to the amino-terminal region of p97, a melanoma surface antigen that is also a member of the transferrin family (*13*) (Fig. 3). The alignment of chicken *Blym*-1 with these transferrin sequences was the same as that previously reported (*2*). The alignment of human *Blym*-1 was fixed by its alignment with chicken *Blym*-1 (Fig. 2). Human *Blym*-1, like chicken *Blym*-1, is related to these amino-terminal transferrin sequences. Significantly, those residues that are conserved between the human and chicken *Blym*-1 genes tend to be conserved among the transferrins as well. If the amino acid sequence of human *Blym*-1 is compared to the amino-terminal region of human transferrin, there are six identities of 39 aligned amino acids ($P < 0.005$) (*11*). Of these six residues, five are also conserved in chicken *Blym*-1. This analysis can be extended to include the other transferrin family sequences. This reveals ten residues of human *Blym*-1 that are conserved in at least one of the transferrin sequences. Seven of these ten amino acids are also conserved between human and chicken *Blym*-1.

Human transferrin and both *Blym*-1 genes display a common pattern of sequence conservation and divergence, with this pattern being somewhat stronger for chicken than for human *Blym*-1 (Fig. 3). For example, the similarity of both *Blym*-1 genes and of human transferrin to other transferrin family sequences is highly conserved in the 5′ half of the indicated sequence but divergent in the 3′ half. Such divergent genes as chicken and human *Blym*-1 are unlikely to have maintained this relationship to transferrin by chance. Rather, the conserved similarity of both *Blym*-1 gene products to transferrin suggests that this relationship reflects some functional property of the *Blym*-1 transforming proteins.

Transferrins are a family of large, iron-binding proteins that are essential growth factors for cultured cells (*14*). A correlation exists between the appearance of transferrin receptors and cell proliferation, suggesting that transferrins may play a role in cell growth (*15*). In support of this concept, it has been shown that transferrin can serve as a lymphocyte mitogen and that blockage of the transferrin receptor with monoclonal antibodies can inhibit cell proliferation even if iron is supplied by alternate mechanisms (*16*). Furthermore, p21, the product of the *ras* transforming gene, has been shown to form a stable complex with the transferrin receptor, suggesting that p21 may exert its effect on cell proliferation in conjunction with transferrin and its surface receptor (*17*). The observed structural relationship between the *Blym*-1 genes and transferrins thus suggests that the *Blym*-1 transforming gene products may also function via a pathway related to transferrin.

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Variation Among Floral Visitors in Pollination Ability: A Precondition for Mutualism Specialization

Abstract. *The unusual floral biology of a neotropical herb provided an opportunity to determine that floral visitors varied significantly in their ability to effect fruit-set. Pollination efficiency and visitation frequency varied among Hymenoptera (five taxa), which were responsible for 99 percent of all fruits set. Lepidoptera (four taxa) were common visitors but poor pollinators. These results indicate that flower visitors vary in their beneficial effects on plants, fulfilling one of the primary conditions required for the specialization of plants on pollinators.*

Despite their ubiquity, mutualisms are perhaps the most poorly understood of all ecological interactions (*1, 2*). Questions of general interest, for which there is little empirical information, include whether potential mutualists vary in quality and what features promote specialization in mutualisms (*2–4*). We report that the visitors to flowers of *Calathea ovandensis* (Marantaceae), a neotropical herb, vary significantly in visitation frequency and their ability to effect fruit-set, two components of pollination efficiency. These results show that the selective effects of potential pollinators on plants can be highly variable, fulfilling one of the primary conditions required for the evolutionary specialization of mutualisms.

The principle of "the most effective pollinator" is central to discussions of plant-pollinator evolution (*3, 5*), but no other study has used seed set as a measure of pollinator efficiency in addition to examining the full range of floral visitors in a natural community (*6–8*). Such an approach is necessary for two reasons: (i) seed set is a direct measure of reproductive success; and (ii) assessment of the relative contribution of each visitor to plant reproductive success requires sampling the entire visitor fauna. Sampling only the most abundant visitors may be misleading if pollination efficiency is not correlated with abundance.

The peculiar floral biology of *Calathea* spp. (*9*) provides an opportunity to determine the pollination efficiency of visitors. Pollen is deposited in a stylar depression behind the stigma before the flower opens. The style is held in tension by a petaloid staminode and is released only when a visitor trips a trigger of thin tissue extending across the nectar tube. Visitors can extract nectar without tripping the flower, but no pollen is deposited or received. When the flower is tripped, the style springs 180° upward to a position where neither stigma nor pollen can contact subsequent visitors. The flower functions in pollen deposition and dispersal only during the tripping process. Flowers survive a single day and, if not tripped by an insect by midafternoon, will sometimes trip themselves, resulting in a low level of self-pollination (*10*).

In a lowland rain forest in Veracruz, Mexico (*11*), we mapped the location of untripped flowers on inflorescences of *Calathea ovandensis*, observed all visits to each flower, and checked flowers after each visit. Flowers tripped by a visitor were marked by coloring the persistent calyx and numbering the adjacent bract; they were censused daily until either the flower had dropped or the fruit had matured.

During 158 hours of observation (*12*), 2574 visits were made by nine major groups of insects. Significant variation among visitors was observed for all estimates of pollination efficiency, including (i) trip efficiency per visit ($\chi^2 = 600$, $P < 0.001$, d.f. = 8), (ii) fruit-set efficiency of tripped flowers ($\chi^2 = 18.6$, $P < 0.005$, d.f. = 5), and (iii) fruit-set efficiency per visit ($\chi^2 = 184$, $P < 0.001$, d.f. = 5) (*13*). Fruit-set is a good index of plant reproductive success because seed number per fruit did not vary among visitors ($\bar{x} = 2.5$, range 1 to 3). Trip efficiency varied from less than 1 percent to 100 percent, and fruit-set efficiency per visit varied from 0 to 36 percent (Table 1). *Euglossa* spp. were the most abundant visitors (52 percent) and accounted for the majority of fruits set (66 percent), even though they did not trip flowers in most visits (80 percent) (Table 1). The second most abundant visitor class, the Hesperiidae, made 21 percent of all visits but were responsible for only 2 percent of all tripped flowers and less than 1 percent of all fruits set (Table 1). Two visitors, *Bombus medius* and *Rhathymus* sp., were jointly responsible for 23 percent of all fruits set but only 5 percent of all visits (Table 1). This result emphasizes that studies considering only the most frequent pollinators may misrepresent the relative contribution to fruit-set and, therefore, the potential selection intensity of individual pollinators on plants.

Hymenoptera and Lepidoptera differed in pollination ability. Hymenoptera were responsible for 71 percent of all visits but 99 percent of all fruits set (Table 1). This difference between visitation frequency and fruit-set was due to the nearly eightfold greater efficiency of Hymenoptera in both tripping and fruit-set of tripped flowers (Table 1). Neither of the two lepidopterans that regularly tripped flowers, *Heliconius ismenius* or *Astraptes* sp., was capable of pollinating *Calathea ovandensis* (Table 1).

Ineffective visitors can reduce plant reproductive success in two ways. First, by extracting nectar without tripping the flower, a visitor may reduce the probability that future visits will be successful. This does not appear to be the case in *C. ovandensis*, where the probability that an insect visit results in a tripped flower is independent of the number of previous visits ($\chi^2 = 2.03$, d.f. = 6, $P = 0.9$) (*14*). Second, tripped flowers cannot receive or donate pollen to future visitors, so taxa that have low fruit-set efficiency of tripped flowers will reduce the reproductive success of their host. However, such insects were either infrequent visitors (*Heliconius ismenius* and *Astraptes* sp.) or rarely tripped flowers (Hesperiidae and *Eurybia elvina*) (Table 1). We conclude that ineffective pollinators in this system have limited negative effect on fruit-set and are primarily commensals, receiving a benefit but providing no benefit in return (*15*).

An increase in the number of visits by efficient pollinators could increase the reproductive success of *C. ovandensis*. Of the 1260 flowers observed in our study, 37.5 percent were tripped by insects, and the fruit-set efficiency of tripped flowers for the entire visitor assemblage was 30.0 percent (141 of 470, Table 1). The product of these two components gives an overall pollinator efficiency of 11.25 percent. By hand-tripping and cross-pollinating 201 unbagged flowers on 9 inflorescences, we achieved 32.3 percent pollination efficiency (100 percent tripped × 32.3 percent fruit-set of tripped flowers). Since the fruit-set efficiency of flowers tripped by insects and by hand was similar (30 and 32.3 percent, respectively), we conclude that changes in tripping efficiency of insect visitors would have the greatest effect on fruit production. The variation among insects in this component of pollination efficiency (Table 1) shows that plants could achieve greater tripping frequency by increasing the number of visits by insects that trip efficiently. For example, even a small change in visitation by *Bombus medius* and *Rhathymus* sp. could influence the reproductive success

Table 1. Visitation frequency and pollination efficiency of insect visitors to *Calathea ovandensis*. Numbers in parentheses give percent of the total number.

Visitor	Visits	Flowers tripped	Fruits set	Efficiency: Trip per visit* (%)	Efficiency: Fruit-set: Tripped flowers† (%)	Efficiency: Fruit-set: Per visit‡ (%)
		Hymenoptera				
Euglossa heterosticta and *E.* sp.	1334 (52)	260 (55)	93 (66)	19.5	35.8	7.0
Eulaema cingulata	216 (8)	59 (13)	12 (9)	27.3	20.3	5.6
Exaerete smaragdina	165 (6)	24 (5)	3 (2)	14.5	12.5	1.8
Bombus medius	38 (2)	38 (8)	13 (9)	100	34.2	34.2
Rhathymus sp.	64 (3)	64 (14)	19 (14)	100	29.7	30.6
		Lepidoptera				
Hesperiidae§	542 (21)	10 (2)	1 (0.7)	1.8	10.0	0.2
Eurybia elvina	120 (5)	1 (0.2)	0 (0)	0.8	0.0	0.0
Heliconius ismenius	72 (3)	7 (2)	0 (0)	9.7	0.0	0.0
Astraptes sp.	23 (1)	7 (2)	0 (0)	30.4	0.0	0.0
Subtotals						
Hymenoptera	1817 (71)	445 (95)	140 (99)	24.5	31.5	7.7
Lepidoptera	757 (29)	25 (5)	1 (1)	3.3	4.0	0.1
Total	2574	470	141			

*(Flowers tripped/flower visits) × 100. †(Fruit-set/flowers tripped) × 100. ‡(Fruit-set/flower visits) × 100. §Includes all taxa except *Astraptes* sp., which is in the Hesperiidae.

of *C. ovandensis* because their trip efficiency was five times that of the most abundant pollinator (Table 1).

In view of the variation in the pollination ability of different visitors, the reproductive success of individual plants is a function of plant characters that determine the number and kinds of visitors that a plant attracts. The extent to which variation in plant fitness is attributable to such characters determines the potential for selection of pollinators on plants (*16*). The observed variation in pollination ability among visitors to *Calathea ovandensis* flowers may be a result of previous selection for specialization, a stage toward further specialization, or both. The demonstration of variation in pollinator ability is an important step in the assessment of how interactions between plants and their potential mutualists can influence the evolution of plant characters and mutualism specificity.

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10. Despite the specialized pollination mechanism, bagged inflorescences in the field as well as unmanipulated inflorescences in an insect-free greenhouse exhibit a low level of fruit-set.
11. The study site was a secondary forest at Laguna Encantada (altitude 350 m) near San Andres Tuxtla (see C. C. Horvitz and D. W. Schemske *Ecology*, in press).
12. Observations were made from approximately 08:30 to 13:30 on 20 days from 27 August to 7 October 1983 during the peak flowering season.
13. In calculating the chi-square statistics for fruit-set efficiency of tripped and visited flowers, all observations for Lepidoptera were grouped to minimize the number of cells with expected values less than 5 [see R. R. Sokal and F. J. Rohlf, *Biometry* (Freeman, San Francisco, 1981)].
14. Tripping probability on the *n*th visit varied only from 0.17 to 0.20 for $n = 1$ to 7.
15. Although Lepidoptera are noted as nectar robbers of *Calathea* spp. (*9*), they do not appear to have a negative effect on *C. ovandensis* at the pollinator stage. However, the larvae of several of these flower visitors have a negative impact on *C. ovandensis* at other stages. Larval *Eurybia* feed exclusively on buds, flowers, and fruits (*11*), while larval Hesperiidae feed on leaves (C. C. Horvitz, unpublished data).
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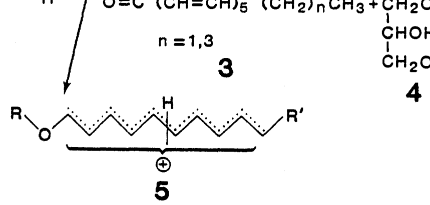
A Model Study of Fecapentaenes: Mutagens of Bacterial Origin with Alkylating Properties

Abstract. *Fecapentaene-14 and -12 are directly acting mutagens that do not require metabolic activation. Their unusual structure suggests a possible mechanism of action. A carbocation that is formed by the addition of an electrophilic species (such as a proton) to the enol ether is most probably the reactive species. A series of model enol ethers with conjugated systems of various lengths was prepared, and a correlation between mutagenicity and increasing reactivity of derived carbocations was found. The glycerol moiety does not play a crucial role in the overall reactivity of the fecapentaenes.*

The results of epidemiological studies (*1*) have indicated that human colorectal cancer is related to the diet and have led to the conclusion that a cancer-causing substance (or substances) may be present in food (*2*). During excretion in feces, this substance would be in contact with the intestinal epithelium long enough to cause neoplastic transformation. The search for such a substance has led to the discovery of four compounds, fecapentaene-14 (**1**) and three stereoisomers of fecapentaene-12 (**2**) (*3–5*) (Fig. 1). The important structural feature of all four substances is their highly unsaturated conjugated enol ether system; this bond system implies that the compounds can be hydrolyzed by an aqueous acid to an unsaturated aldehyde (**3**) and glycerol (**4**) (Fig. 1a), from which they are formally derived. The acid protonates the enol ether to give a carbocation (**5**) (Fig. 1a) that will then undergo a series of rapid rearrangements and transformations (*6, 7*). The propensity for the formation of such a cation (or cations, since several



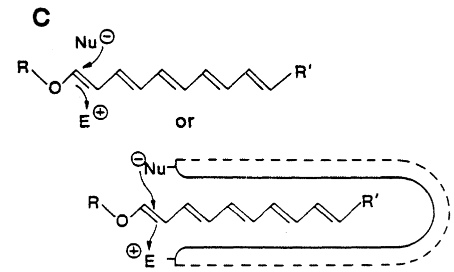


Fig. 1. (a) Scheme of carbocation (**5**) formation from fecapentaenes (**1**, **2**) and related model substances (for example, compound **1** with $R = CH_3$ and $R' = H$). (b) Subsequent acetal (**6**) formation [see (*18*)]. (c) A more general depiction of (a) in which $E^{\oplus}$ and $Nu^{\ominus}$ can be parts of the same molecule (for example, a nucleic acid or a protein), resulting in intramolecular linking. The formulas have no configurational or conformational implications and may represent several combinations of *cis-trans* geometries [see (*3*)].