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A MODEL AND LEXICON FOR POLLEN FATE[1]

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As pollination biology undergoes unprecedented growth as a discipline, confusion in the use of terms has become increasingly common. The need for a flexible yet unambiguous terminology has become urgent. As an example we discuss how the term "pollination efficiency" is used differently by 18 studies, and "pollinator effectiveness" by seven others. Here we present flowcharts of two general models of pollination systems (biotic and abiotic) that trace all the events from pollen production to development of seed or fruit, and we develop a lexicon for the quantities of pollen, processes of transfers (to a vector, to a stigma), and ratios of quantities that are of interest in studies of pollination and mating systems. An appendix includes a glossary of the definitions we suggest.

Although pollination biology is not a new field, older ideas are rapidly being refined and/or expanded into new concepts, and modern techniques are encouraging new types of investigations. Since the 1970s there has also been a growing integration of studies of pollination and mating systems. This disciplinary and interdisciplinary growth has led to the coining of many new terms, as well as the use of old ones in new ways. Tracing developments in the literature has become difficult because of inconsistent and ambiguous use of words. We give three examples of this ambiguity, and then develop a model and lexicon of the possible fates of pollen that include, but are not restricted to, pollination.

One example of ambiguity is the word "pollination" itself. Strictly speaking, pollination in angiosperms has three phases: 1) release of male gametophytes (pollen) from the male part of a flower; 2) transport from the pollen source to pollen recipient; and 3) deposition of pollen on a stigma (Faegri and van der Pijl, 1979). Pollination can be followed by germination of the pollen grain, and then by fertilization. Authors commonly but inadvisedly lump all of these processes under the single title of "pollination." Following Faegri and van der Pijl (1979), we restrict our use of the word pollination to the three phases listed above, but we also include the other two processes in our lexicon because many authors use pollen germination and seed set or fruit set as measures of successful completion of pollination.

As another example of ambiguity in terminology, consider the term "pollination efficiency"; it has been used in at least 12 different ways in 18 studies since 1972. Levin and Berube (1972) may have been the first to use the term, which they used in a broad sense to represent the difference between the amount of pollen picked up by a pollinator and the number of pollen tubes in a style (they quantified several steps in this process). Kendall and Smith (1975, 1976) considered pods and beans produced per visit (for *Vicia faba*) or percent fruit set (for *Phaseolus coccineus*) as measures of pollination efficiency. Tepedino (1981) also used the term to refer to fruit and/or seed set per flower visit, but suggested that it should include consideration of three components: number of visits required for pollination, numbers of pistillate and staminate flowers visited in a monoecious species, and the average time spent visiting single flowers. Parker (1981, 1982) used the term to refer to the number of seeds that result from the visit by a single pollinator to an onion or sunflower inflorescence that is bagged before and after the visit and only exposed when receptive. Schemske and Horvitz (1984) considered pollinator visitation frequency, the frequency with which *Calathea ovandensis* flowers were tripped by visitors, the fruit-set efficiency of tripped flowers, and fruit-set efficiency per visit as ways to estimate pollination efficiency; they also calculated pollination efficiency as the product of the percentage of flowers tripped by insects and the fruit-set efficiency of tripped flowers. Jennersten (1984) didn't define what he meant by the term, but referred to Levin and Berube (1972) and was concerned primarily with numbers of pollen grains on butterflies' bodies. Dafni, Eisikowitch, and Ivri (1987) measured pollination efficiency in two ways: as the percentage of stigmas touched in a series of visits by different insects, and as fruit set. Richards (1987) equated pollinator efficiency with foraging rate, or the time that it took a pollinator or flower visitor (e.g., nectar robber) to visit ten to 50 flowers. Andersson (1988) considered pollination efficiency from the perspective of the plant being visited, rather than the pollinator, using the term in the context of the inflorescence size that will maximize the interaction between visitation rate and pollination in a self-incompatible plant. Galen and Newport (1987) and Waser and Price (1990) used the same term to refer instead to the amount of pollen transferred to a stigma by a single visit (i.e., effect on seed set), thus restricting it to a measure of individual pollinator performance. Cruden et al. (1990) defined it as the number of pollen grains deposited per stigma, divided by the number of grains produced per flower, or an index of efficiency from the perspective of the plants producing and receiving the pollen. Guo et al. (1990) called the percentage of stigmas with germinating

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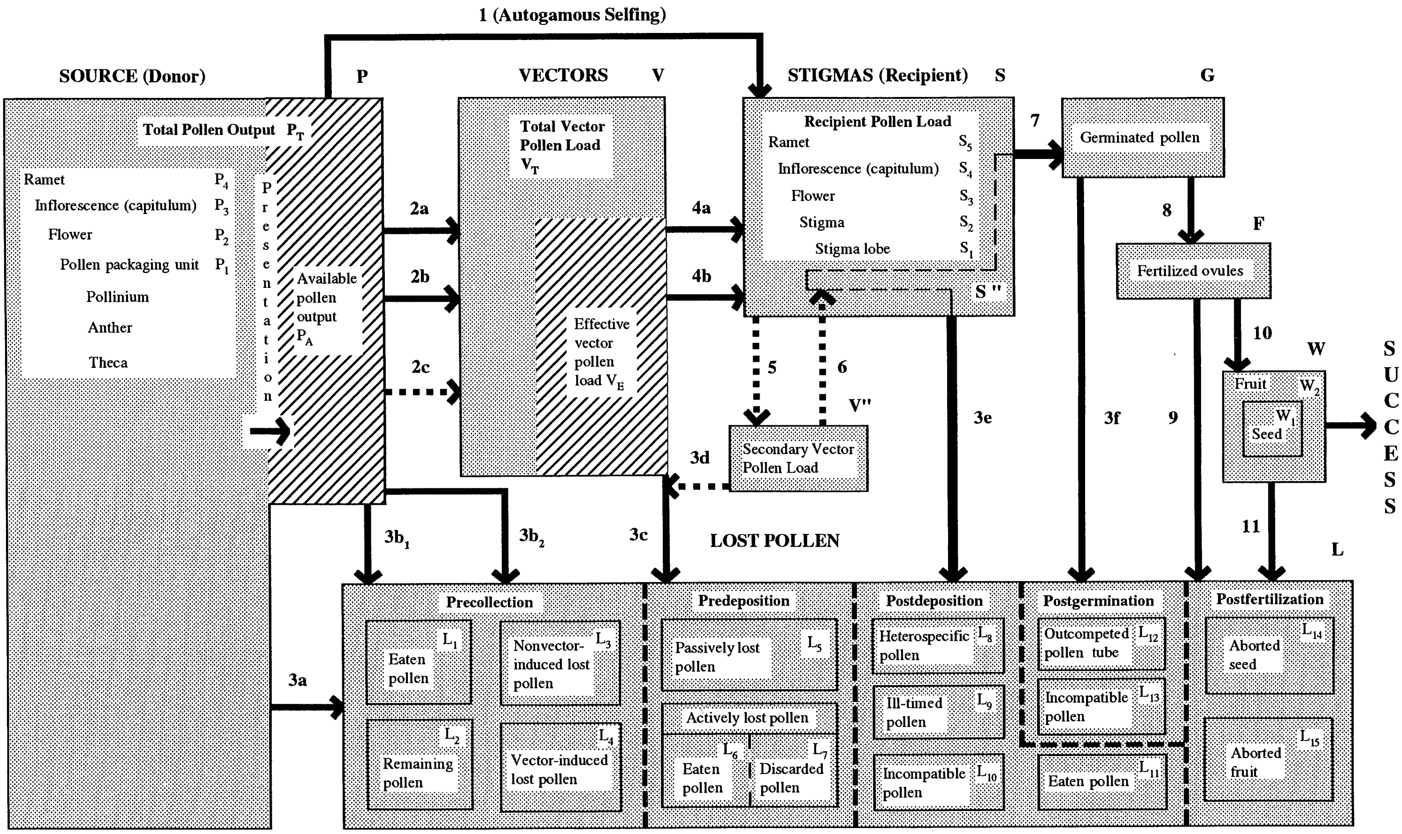

Fig. 1. A flow chart for biotic pollination describing the various paths that pollen can take after production, including successful pollination and seed production as well as potential sources of loss. See Table 1 for the terms we propose for quantities in boxes, Table 2 for the terms for processes (arrows between boxes), and Table 3 for definitions of ratios of quantities in boxes. The dotted lines indicate secondary transfers of pollen that may involve minimal quantities of pollen.

pollen grains pollination efficiency. Macfarlane, van den Ende, and Griffin (1991) used both "pollinating efficiency" and "pollinating effectiveness" to refer to the proportion of honey bees that were collecting pollen, in contrast to nonpollinating nectar foragers. Velthuis and Cobb (1991) never actually detailed how they would calculate pollination efficiency, but reported that the following behaviors were relevant to measuring it: the number of flights observed by bumblebees leaving a nest box, the number of flowers visited, and the sequence in which male and female plants were visited. Van Praagh and Hauschildt (1991) compared three pollination treatments for pollination efficiency by measuring the number of fruits produced per 100 flowers. In addition to this variation in use of "pollination efficiency," "pollinating efficiency" has also been used in a similar context (e.g., Free, 1966).

A final example of ambiguity in a commonly used term is "pollinator effectiveness." For example, "Effectiveness measures are based on what is accomplished by a single visit by a particular animal, including effectiveness per visit at removing pollen from anthers, depositing it on stigmas, producing seeds, or influencing other aspects of reproduction" (Young, 1988; see references she cites that have used these different measures). Young (1988) actually measured pollinator effectiveness as "the contribution to seed set per individual beetle." Motten (1986) measured pollinator effectiveness in two ways. For some species he used the percent fruit set and number of seed set resulting from a single visit of a pollinator to a previously (and subsequently) bagged flower. For other species he counted pollen tubes that reached the base of the style following a single pollinator visit. Spears (1983) proposed a quantitative measure of pollinator effectiveness, also based on seed set, but measured at the level of the plant population. He also made the distinction between "indirect" measures of pollinator effectiveness, based on examination of pollen carried by flower visitors, and "direct" measures such as the one he proposed, based on seed set in response to pollinator visits. Neff and Simpson (1990) defined pollinator effectiveness (or efficacy) as "the numbers of successful pollinations expressed as the percent of available florets pollinated per visit." Macfarlane, van den Ende, and Griffin (1991) used the term synonymously with "pollination efficiency," to refer to the proportion of honey bees that were collecting pollen, in contrast to nonpollinating nectar foragers. Galen and Newport (1987) defined it as a measure comprising at least two components: visitation rate and pollination efficiency. Fenster (1991) measured conspecific stigma pollen loads and the ratio of number of bees to number of flowers in plots as indices of pollinator effectiveness.

As illustrated above, the term "pollination efficiency" has already become a panchreston, with such flexible meaning that it is "as likely to generate confusion as to

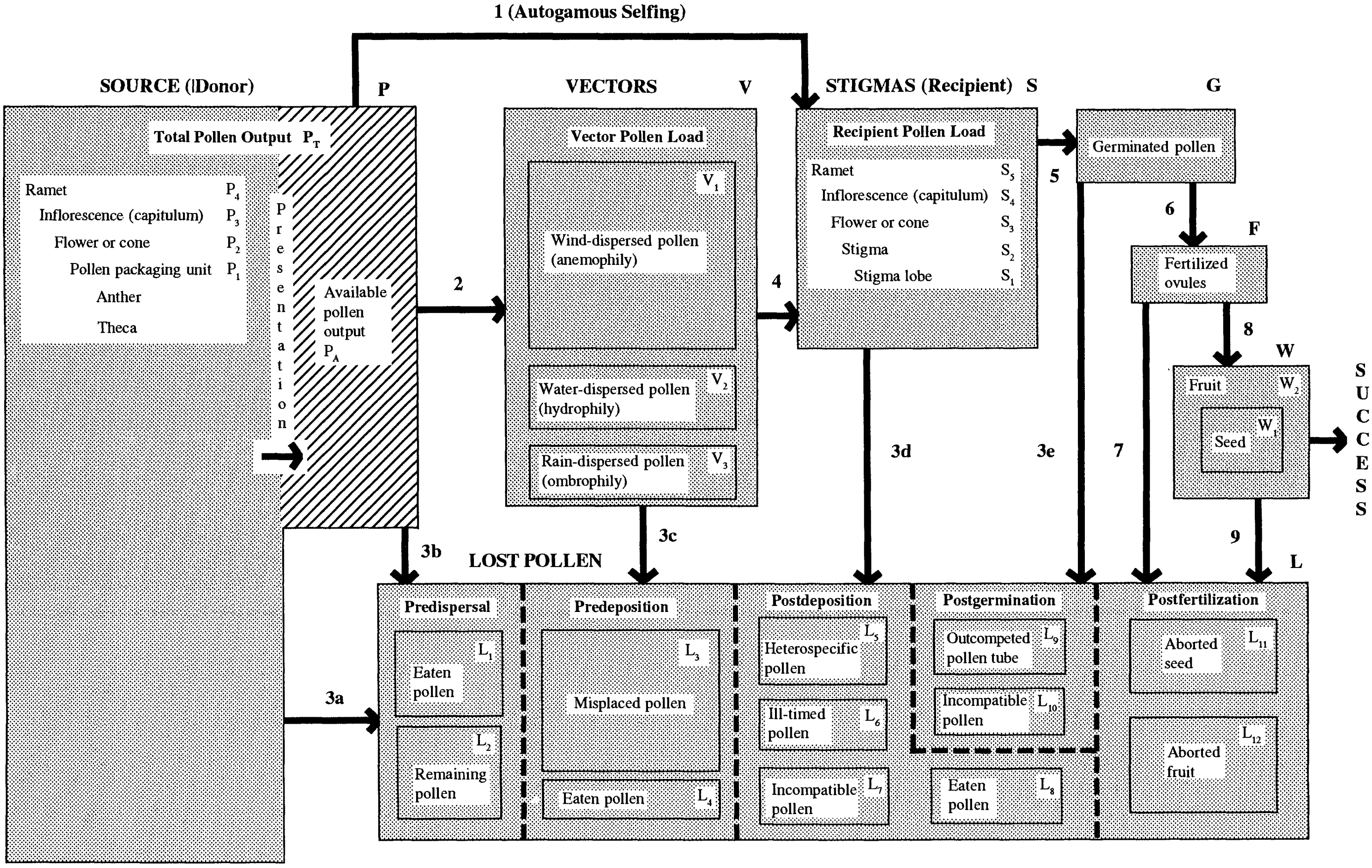

Fig. 2. A flow chart for abiotic pollination describing the various paths that pollen can take after production, including successful pollination and seed production as well as potential sources of loss. See Table 1 for the terms we propose for quantities in boxes, Table 2 for the terms for processes (arrows between boxes), and Table 3 for definitions of ratios of quantities in boxes.

communicate information" (Simberloff and Dayan, 1991), and other terms run the same risk (e.g., Inouye, 1980). In this paper we offer a standardization of vocabulary that we hope will facilitate communication among pollination biologists. We do so by first presenting a general conceptual model for the fate of pollen, and second by developing a lexicon for the important, or at least commonly discussed features of the model. The model is illustrated by two flowcharts showing the potential paths pollen can take via biotic (Fig. 1) and abiotic pollination (Fig. 2). The flowcharts diagram all the various stages and processes between pollen production in anthers and development of seeds or fruits. There are many mechanisms by which the transfer of gametophytes from a pollen donor to a vector and from a vector to a pollen recipient can occur, including both active and passive mechanisms by pollinators or by plants. These mechanisms can be categorized, and we offer a vocabulary (summarized in Appendix 1) for this classification, covering the sequence of processes, the quantities of pollen, and ratios of pollen volumes involved in the models. More specific terms can also help to avoid the ambiguity associated with more general ones.

The description of the models in the text is organized into six sections: I. Production and presentation of pollen; II. Transfer to, and transport by vectors; III. Deposition on and acquisition by stigmas; IV. Pollen grain germination and fertilization of ovules; V. Losses of pollen from the system; and VI. Common ratios of pollen quantities.

We first trace the fate of pollen deposited on stigmas, noting as we go the words or phrases that we recommend. We call attention to the similarities and differences found in the abiotic and biotic flowcharts. We then describe the fates of pollen on unsuccessful pathways, and the mechanisms by which pollen is lost from the pollination system.

THE MODELS (FIGS. 1, 2)

Each of the boxes in the charts represents a quantity of pollen that can flow through or out of the pollination system, and the relative size of the box is meant to represent qualitatively the amounts of pollen at the various stages. Arrows between the boxes indicate pathways in which pollen is moved from box to box. Associated with each chart are three tables of vocabulary: Table 1 lists the boxes and names we have assigned to the quantity in each box, Table 2 lists the pathways and their names, and Table 3 shows the terms for measurements of the ratios of some pairs of boxes. Suggested terms are boldfaced in the text. In some cases we suggest that the same process have two different names, depending on whether it is described from the plant's perspective or that of a vector.

TABLE 1. Terms suggested for the identities of boxes in Figs. 1 (biotic pollination) and 2 (abiotic pollination).

Biotic	Abiotic	Contents of the box
P (Pollen Output)		
P_1	P_1	Pollen output per pollen packaging unit, e.g., per theca, anther, or pollinium
P_2	P_2	Pollen output per flower or cone
P_3	P_3	Pollen output per inflorescence (capitulum)
P_4	P_4	Pollen output per ramet
P_T	P_T	Total pollen output
P_A	P_A	Available pollen output; a subset of P_T
V (Vector Pollen Load)		
V_E		Effective vector pollen load; a subset of V_T
V_T		Total vector pollen load
V''		Secondary vector pollen load
	V_1	Anemophilous pollen
	V_2	Hydrophilous pollen
	V_3	Ombrophilous pollen
S (Pollen on Stigmas)		
S_1	S_1	Stigma lobe pollen load
S_2	S_2	Stigma pollen load
S_3	S_3	Gynoecium pollen load
S_4	S_4	Inflorescence (capitulum) pollen load
S_5	S_5	Ramet pollen load
S''		Secondary stigma pollen load
L (Lost Pollen)		
L_1	L_1	Eaten pollen
L_2	L_2	Remaining pollen
L_3		Nonvector-induced lost pollen
	L_3	Misplaced pollen
L_4		Vector-induced lost pollen
	L_4	Eaten pollen
L_5		Passively lost pollen
L_6		Postcollection eaten pollen
L_7		Discarded pollen
L_8	L_5	Heterospecific lost pollen
L_9	L_6	Ill-timed pollen
L_{10}	L_7	Incompatible pollen (stigmatic incompatibility)
L_{11}	L_8	Eaten postdepositional pollen
L_{12}	L_9	Outcompeted pollen tube
L_{13}	L_{10}	Incompatible pollen (stylar incompatibility)
L_{14}	L_{11}	Aborted seed
L_{15}	L_{12}	Aborted fruit
G (Germinated Pollen)		
G	G	Germinated pollen load
F (Successful Pollen)		
F	F	Fertilized ovules
W (Seed and Fruit)		
W_1	W_1	Seed set
W_2	W_2	Fruit set

TABLE 2. Terms suggested for the pathways between boxes in Figs. 1 (biotic pollination) and 2 (abiotic pollination). If the same pathway can lead to multiple boxes, the boxes are specified in parentheses after the pathway name.

Biotic	Abiotic	Pathway
1	1	Autogamous selfing
2	2	Transfer of pollen from source to vector; plant and animal perspectives include:
2a	2	Pollen placement (placed on the vector by flower; can be passive or active)
2b		Pollen collection (gathered by the vector; can be passive or active)
2c		Secondary pollen transfer
3a (L_1)	3a (L_1)	Prepresentation pollinivory (pollen never made available for dispersal)
$3b_1$ (L_2)		Postpresentation lack of collection.
	3b (L_2)	Postpresentation lack of dispersal
$3b_1$ (L_1)	3b (L_1)	Postpresentation pollinivory (pollen was available for dispersal)
$3b_2$ (L_3)		Nonvector-induced pollen loss
$3b_2$ (L_4)		Vector-induced pollen loss
	3c (L_3)	Pollen misplacement (pollen never lands on a stigma)
3c (L_5)		Passive vectorial pollen loss, via gravity or shear forces
3c (L_6)	3c (L_4)	Predeposition pollinivory (eaten directly or groomed off and fed to larvae)
3c (L_7)		Pollen discarding, by the vector (grooming)
3d (L_5)		Passive vectorial pollen loss, via gravity or shear forces
3d (L_6)		Predeposition pollinivory (of secondary pollen)
3d (L_7)		Pollen discarding, by the vector (grooming of secondary pollen)
3e (L_8)	3d (L_5)	Heterospecific pollen deposition (biotic: primary or secondary pollen)
3e (L_9)	3d (L_6)	Unreceptive pollen deposition (biotic: primary or secondary pollen)
3e (L_{10})	3d (L_7)	Incompatible pollen deposition (biotic: primary or secondary pollen) (stigmatic incompatibility)
3e (L_{11})	3d (L_8)	Postdeposition pollinivory (biotic: primary or secondary pollen)
3f (L_{12})	3e (L_9)	Pollen tube competition
3f (L_{13})	3e (L_{10})	Incompatible pollen deposition (stylar incompatibility)
4	4	Transfer of pollen from vector to stigma
4a	4	Pollen acquisition (from the plant's perspective); active or passive
4b		Pollen deposition (from vector's perspective); active or passive
5		Secondary pollen placement, or pollen collection (S to V″)
6		Secondary pollen acquisition, or pollen deposition (V″ to S″)
7	5	Germination
8	6	Fertilization
9 (W_1)	7 (W_1)	Seed development; seed set
9 (W_2)	7 (W_2)	Fruit development; fruit set
10 (L_{14})	8 (L_{11})	Seed abortion
10 (L_{15})	8 (L_{12})	Fruit abortion

I. Production and presentation of pollen—Pollen produced by a **pollen donor**, or **source**, is **pollen output**. Most, if not all of the **pollen output** is then presented by dehiscence and in floral displays. For many kinds of studies production of pollen could be measured at subanther levels (e.g., theca), or more inclusive levels, e.g., flowers, inflorescences, ramets, or genets. Examples of these latter levels are represented as P_1, P_2, P_3, and P_4, respectively, in both Figs. 1 and 2. At each of these levels P_T stands for the **total pollen output**; e.g., the total amount of pollen produced and presented per anther, per flower, etc. The **total pollen output** may not be available for dispersal at a given time, however, depending on the pollen presentation schedule (Thomson and Thomson, 1992). The subset that is available at a given time is indicated as P_A (**available pollen output**). Pollen enclosed in an anther makes a transition (the process of presentation) to **available pollen** as the anther dehisces over some period of

TABLE 3. Terms suggested for the ratios of one box to another in Figs. 1, 2. Many of these could be measured per vector visit, vector species, ramet, etc., and are recommended for comparisons among vectors, plants, or populations. All of the ratios except secondary efficiencies have a range of 0–1.0 and relate quantities of pollen toward the right side of the figures to quantities on the left. A few other ratios discussed in the text but not shown in the figures are also included here. Most of these ratios can be converted to rates by scaling to an appropriate unit of time.

Ratio	Term
1. Denominator: **Pollen output at source** (can be calculated using total (P_T) or available (P_A)).	
$\frac{V}{P}$	= placement efficiency (from plant's perspective when pollen is transferred to the vector by the flower)
$\frac{V}{P}$	= collection efficiency (from vector's perspective (not applicable to Fig. 2))
$\frac{V_E}{P}$	= effective placement (or collection) efficiency
$\frac{T}{P}$	= dispersal efficiency (numerator is the total number of stigmas upon which pollen from a designated source has landed). Numerator could be S_1–S_5.
$\frac{S}{P}$	= source efficiency
$\frac{F}{P}$	= fertilization efficiency
$\frac{W_1}{P}$	= siring efficiency
$\frac{L}{P}$	= pollen loss ratio (specify level as P_1–P_4)
2. Denominator: **Vector pollen load**	
$\frac{S}{V}$	= vector pollinating efficiency; can be calculated as total (V_T) or effective (V_E)
$\frac{F}{V}$	= vector fertilization efficiency
$\frac{W_1}{V}$	= vector seed set efficiency
$\frac{W_2}{V}$	= vector fruit set efficiency
$\frac{V''}{S}$	= secondary transfer efficiency (not applicable to Fig. 2)
$\frac{S''}{V''}$	= secondary vector efficiency (not applicable to Fig. 2)
3. Denominator: **Number of ovules**	
$\frac{S}{\# \text{ ovules}}$	= stigma pollen–ovule ratio
$\frac{F}{\# \text{ ovules}}$	= ovule fertilization efficiency
$\frac{W_1}{\# \text{ ovules}}$	= ovule seed set efficiency
$\frac{P_2}{\# \text{ ovules}}$	= pollen–ovule ratio (Cruden, 1977)
4. Denominator: **Stigma pollen load**	
$\frac{G}{S}$	= germination efficiency; can be calculated per stigma lobe, stigma, etc.
$\frac{F}{S}$	= stigma fertilization efficiency; can be calculated per stigma lobe, stigma, etc.
$\frac{W_1}{S}$	= stigma seed set efficiency; can be calculated per stigma lobe, stigma, etc.
$\frac{W_2}{S}$	= stigma fruit-set efficiency; can be calculated per stigma lobe, stigma, etc.
5. Denominator: **Fertilized ovules, seeds,** and **fruits**	
$\frac{L_{14}}{W_1}$	= seed abortion rate
$\frac{L_{15}}{W_2}$	= fruit abortion rate

time; similarly, the multiple anthers of some flowers may present pollen over a period of days. Kearns and Inouye (1993) summarize methods that could be used to measure P_A or P_T.

Pollen produced by plants with abiotic pollination (Fig. 2) follows many of the same processes of production and packaging at the level of the androecium and presentation by flowers. In self-pollinating species presentation of pollen to a vector is often deleted from this sequence. Presentation of pollen on the anthers (or other site in secondary pollen presentation—see next section) completes the first phase of pollination, sensu strictu (Faegri and van der Pijl, 1979).

II. Transfer to, and transport by vectors*—Biotic pollination (Fig. 1)*—The second phase of pollination involves both the transfer of pollen from the **source** to the **vector** and transport by the vector to a pollen recipient. From the plant's perspective this transfer is called **pollen placement** (pathway 2a); this same transfer from the perspective of the vector is called **pollen collection** (pathway 2b). From either perspective this transfer can be passive or active. A common example of **passive pollen placement** by flowers is the dusting of pollen on vectors as they visit flowers while foraging for nectar or pollen. Floral trigger mechanisms that actively place a pollinium or pollen on a vector are examples of **active pollen placement** by flowers; some species with such mechanisms are listed in table 7-2 in Kearns and Inouye (1993).

As flower visitors forage for nectar or pollen as a resource, much pollen can accumulate on their bodies without directed behaviors of the vector; we call this common process **passive pollen collection**. Pollen transfer is also accomplished by the pollinators actively collecting pollen and placing it on their bodies (**active pollen collection**, path 2b). One familiar example of **active pollen collection** is buzz pollination in Solanaceae, Caesalpinaceae, and Primulaceae (e.g., Buchmann, 1983), in which bees vibrate their wing musculature and bodies at a pitch that shakes pollen from poricidal anthers onto their bodies. Often the behavior of the pollinator is directed to collecting pollen for delivery and consumption at a nest. But in at least two extraordinary cases pollinators use some behavior specifically for pollen collection, but do not use the pollen as food. This behavior is known presently from only two systems—*Tegeticula* moths that pollinate *Yucca* flowers (e.g., Aker and Udovic, 1981; Powell, 1992) and fig wasps (Wiebes, 1979). Galil (1973) coined the term "ethodynamic pollen collection" to describe this phenomenon.

The pollen that is placed on or that is collected by a vector is called a **vector pollen load**; it can be measured either by counting pollen grains or determining its mass. Some of the pollen on a vector's body, such as that placed in a corbiculum or other pollen-carrying structure and later consumed, is effectively removed from the pollination process. Thus, we suggest **effective vector pollen load** as a term to refer to the subset of pollen grains on the vector's body that are in a spot from which they can be transferred to a stigma.

Transfers of pollen from **source** to **vector** may not always be direct. In some cases pollen may be released from an anther, accidentally dislodged and misplaced on another part of the flower, and then secondarily transferred to the pollinator (**secondary pollen transfer**). In the case of species with loose, buoyant pollen, it is not uncommon for the activities of foraging flower visitors to **dislodge** dehiscent pollen from the anthers, and generate a dusting of other flower parts with pollen. As potential pollinators visit the flower subsequently, this loose pollen may adhere to the vector in an unintended, yet effective, secondary transfer.

The phrase we suggest, **secondary pollen transfer**, is similar to but different from the previously established term **secondary pollen presentation** (see Appendix 1). The latter implies functional and/or adaptive features of the flower that enhance the placement of pollen on the vector, whereas our term applies to the process of accidental recovery of dislodged pollen that would otherwise be lost from pollination. Many examples of adaptive **secondary pollen presentation** are known (Yeo, 1993): in some species of Rubiaceae (Nilsson et al., 1990), pollen is shed from the anthers onto the exterior of the style shortly before anthesis. In *Banksia* (Proteaceae) pollen is normally dehisced onto the "pollen presenter," a specialized region of the style, just before the flower opens (Vaughton and Ramsey, 1991). In Marantaceae, pollen from the single functional stamen is placed on the stigma prior to anthesis and from there onto a hymenopteran visitor by the tension-spring of the style (Kennedy, 1973), an example of **active pollen placement**.

If pollen is not transferred to a vector it may still serve to self-pollinate (path 1, **selfing**); delayed selfing is one example of this (Lloyd, 1979). Shedding of the corolla (e.g., monkey flower, *Mimulus guttatus*; Dole, 1990, 1992) or wilting of the petals (e.g., Bee orchids, *Ophrys apifera*; Darwin, 1877b) results in delayed selfing. Cleistogamy is another example of autogamy, but involves pollen that is never made available to a vector. This transfer of pollen is not necessarily a passive process; in *Mirabilis* self-pollination of cleistogamous flowers is an active process in which the style elongates 1–3 mm and curls, thereby brushing the stigma by the anthers (Cruden, 1973).

Abiotic pollination (Fig. 2)—Many of the terms we propose for use in descriptions of the second phase of abiotic pollination are similar to those described for biotic pollination, so we describe only those that are different. See Tables 1–3 for a complete lexicon.

Instead of an animal vector facilitating the transport of pollen to receptive stigmas, successful abiotic pollination involves vectors such as wind (**anemophily**), water (**hydrophily**), or perhaps even rain (**ombrophily**; Faegri and van der Pijl, 1979). Dehiscence may directly lift the pollen into the fluid medium, such as air in wind-pollinated species (e.g., Graminae, Fagaceae) or water in water-pollinated species (e.g., Potamogetonaceae). Some minor indirect steps (not included in Fig. 2) may also occur. The loose, buoyant pollen of most wind-pollinated species is often dusted on other flower parts, such as glumes, bracts, or leaves. Subsequent gusts of wind may lift this loose pollen from such nonflower structures secondarily into the wind, an act of **secondary pollen dispersal**. Analogous processes doubtless occur in hydrophily and ombrophily.

III. Deposition on and acquisition by stigmas—*Biotic pollination (Fig. 1)*—Pollen adhering to an animal vector has one favorable fate, i.e., **deposition** on a conspecific, receptive, compatible stigma. The transfer of pollen from vector to stigma can be viewed either from the plant's perspective (**acquisition**; path 4a) or the vector's (**deposition**; path 4b). In nearly all species of plants that use animal vectors, this favorable outcome, or generation of a **stigma pollen load**, is accomplished by pollen grains being deposited *passively* (**passive deposition**) by the vector during a visit to a functionally female conspecific flower. The passivity of the deposition is from the point of view of the vector, i.e., it is visiting the flower for other reasons (such as foraging for floral resources) rather than intentionally pollinating the flower. Only in the case of yucca or fig pollination is pollen actively transferred to the stigmas by the insect (**active pollen deposition**; which we suggest as a replacement for "ethodynamic pollination"; Galil, 1973).

The anatomical arrangement of flower parts may facilitate **passive pollen acquisition** by a stigma even though no actual movement of flower parts occurs; hence the acquisition is passive from the plant's perspective. For example, *Pedicularis groenlandica* Retz has the style elongated and curved in a way that effectively brings the stigma onto the anterior abdominal surface of visiting *Bombus* bees, where a concentration of ungroomed pollen, the **effective vector pollen load**, is likely to reside (Macior, 1968). Pollen (or pollinia) can be effectively removed from pollinators by protuberances on the style or column (in orchids) as the animal visits the flower.

In contrast, some plant species have devices near or on the stigma that directly pluck the pollen off the vector and effectively position the pollen on a receptive stigma. We define **active pollen acquisition** by a plant to be those actions that bring mechanical motion into play in the retrieval of pollen (or pollinia) from the vector; this includes the subset of pollination syndromes described as movement herkogamy (Webb and Lloyd, 1986) when it is the pistil that moves. For flowers that have a trip or spring mechanism, like the snap-coiled style in the Marantaceae, the pistonlike action of fabaceous legumes, and the catapult of *Drakaea* orchids, the process of **active pollen acquisition** occurs simultaneously with **active pollen placement** (Section II above).

The pollen deposited is the **stigma pollen load** (box S). The several hierarchical levels of structure in the pollen recipient (lobe, stigma, gynoecium, capitulum, inflorescence) require that **stigma pollen loads** should be specified to level, e.g., **inflorescence pollen load**. Moreover, there is a variety of morphological arrangements of stigmas, styles, carpels, and ovules in flowers that ultimately influence interpretations of reproductive success. These can include: 1) multiple lobes on a single stigma; 2) a single stigma leading to a single ovule in a carpel; 3) a single stigma leading to multiple ovules in a single carpel; 4) multiple stigmas any of which can lead to any ovule in an ovary; and 5) multiple stigmas and styles each of which only leads to one locule among many.

The first case, a **stigma lobe pollen load**, is of interest because a **threshold germination number** may be required for pollen germination (Schemske and Fenster, 1983). A **stigma pollen load** may refer to pollen on the single stigma of some flowers, or on each stigma of a flower with multiple stigmas. *Passiflora vitifolia* is an example of a species with multiple stigmas and a single ovary; pollen deposited on any stigma may fertilize ovules in any part of the ovary (Snow, 1982). *Aquilegia caerulea* is an example of a species with multiple carpels in a flower and separate stigmas and styles attached to each of them (Montalvo, 1992). In both of these cases the pollen on any single stigma is a **stigma pollen load**, while the total pollen on all stigmas of a flower is a **gynoecium pollen load** (S_3). For comparisons among inflorescences, summing of the appropriate constituent pollen loads would generate the **inflorescence pollen load** (S_4). Similarly, in composite flower heads of the Asteraceae the pollen loads on all the component florets taken together form the **capitulum pollen load** (S_4).

There exists the potential for a repeating pathway (paths 5 and 6) for postdepositional pollen to be retransported and redeposited through **secondary pollen deposition**. By this we mean that part of a **primary stigma pollen load** could be picked up by a secondary vector, transported (through **secondary pollen dispersal**) as a **secondary vector pollen load** (box V″) to a second stigma, and deposited (**secondary pollen deposition**, path 6) as a **secondary stigma pollen load** (box S″) (e.g., Svensson, 1986). Although our knowledge of the dynamics of pollen has barely reached this stage, there is the potential that this cycle of pollen transfer and redeposition could be repeated. However, because pollen that enters this cycle is once again subject to a variety of possible losses before successful redeposition on another stigma, there might be selection on both **pollen donor** and **pollen recipient** to minimize the possibility of this cycle.

Abiotic pollination (Fig. 2)—Successful pollen deposition (path 4) in the abiotic model occurs purely by the landing of vector-borne pollen on receptive stigmas.

IV. Pollen grain germination and fertilization of ovules—The endpoint of **pollination** as defined by Faegri and van der Pijl (1979) and in this lexicon is the deposition of pollen on the stigma by the vector; at this point the vector-mediated transport has ended. However, so many studies of pollination biology are concerned with Darwinian fitness of individuals that investigators are quite naturally impelled to measure success of pollination in terms of offspring produced (e.g., fertilized ovules, number of embryos, number and size of seeds, number and size of fruits, etc.). For this reason we include in our models the postdepositional processes of **germination** of pollen grains on the stigma, the successful growth of pollen tubes down the style and through the micropyle, and **fertilization** of an ovule (all together implied by paths 7 and 8 (Fig. 1; paths 5 and 6 in Fig. 2). Box F is the number of successfully **fertilized ovules**. Thereafter, **seed set** (box W_1) and/or **fruit set** (box W_2) is achieved by proper development of the sporophyte (path 9 in Fig. 1, path 7 in Fig. 2). Interpretation of fruit production may be confusing in those cases where fruit production is induced without seed set.

V. Pollen losses—Pollen is lost from pollination systems at every possible stage and transition in both models. In many cases the quantity of lost pollen can be tremendous; the likelihood of a pollen grain getting from its source in the anther to its final destination of fertilization of an ovule may be infinitesimally small. For example, Harder and Thomson (1989) reported that nectar-gathering bumblebees deposited on average only 0.6% of the pollen grains removed from *Erythronium grandiflorum* (Liliaceae) flowers onto the stigmas of subsequently visited flowers.

Biotic pollen losses (Fig. 1)—At the **source** level (production and presentation in anthers and flowers) pollen is lost from pollination when it is not transferred to vectors (or used in selfing). We call these **precollection pollen losses**. Three processes that contribute to **precollection pollen loss** are **pollinivory**, **lack of collection**, and **induced pollen loss**. In **prepresentation pollinivory** (path 3a) or **postpresentation pollinivory** pollen is eaten directly from an anther or pollinium, or other site of presentation; the quantity of pollen lost is **eaten pollen** (box L_1). The agents of pollinivory may be thieves or robbers (Inouye, 1980) not involved in pollination at all, or may be the effective pollinators themselves; the implications for the course of action of natural selection to reduce the loss may be different if pollinators rather than thieves are responsible for the loss. **Remaining pollen** (box L_2) is a consequence of **postpresentation lack of collection** (path $3b_1$); this pollen was available but never left the pollen donor and is not used for delayed selfing. The quantity of **remaining pollen** lost because of lack of dispersal can be substantial (Vaughton and Ramsey, 1991); for example, many species of orchids appear to have very low rates of visits by pollinators, so that orchid pollinia are often left in place (e.g., Darwin, 1877b; Gill, 1989). Pollen may be dislodged from anthers and fall into places not conducive for subsequent collection. Dislodgement can be caused by wind or rain blowing or washing pollen out of anthers (**nonvector-induced pollen loss**; path $3b_2$), or the activities of flower visitors (**vector-induced pollen loss**; path $3b_2$). In cases such as buzz pollination, in which a cloud of pollen is generated by a pollinator, much of the pollen may not land on the vector but instead may be lost when it lands on the perianth or other plant parts, and/or falls into inaccessible places from which it can't be transferred (such as the ground). These quantities are **nonvector-induced**

lost pollen (box L_3) and **vector-induced lost pollen** (box L_4).

Pollen losses can also occur during transport on the animal vector. Broadly these can be called **predeposition pollen loss**. Pollen that is loosely adherent to the pollinator can passively fall off the vector as it moves around on a flower or flies (or walks) to another flower. During transport on a flying animal vector, wind can shear pollen off the body (path 3c, **passive vectorial pollen loss**; quantity L_5, **passively lost pollen**). In contrast, **active vectorial pollen loss** (path 3c) occurs as a consequence of directed behaviors of the pollinator. For example, dehisced pollen may be collected directly from anthers and packed into a pollen-carrying structure (e.g., a bee's corbiculum). This pollen may be eaten later by the vector itself or its brood in a nest (quantity L_6, **postcollection eaten pollen**). Note that this avenue of loss differs from path $3b_1$ (**postpresentation pollinivory**) only in that the pollen already has been transferred by the vector, instead of eaten from the anthers. An animal vector may also actively discard pollen from its body because of some unsatisfactory feature such as unsuitability for consumption (**pollen discarding**; **discarded pollen** quantity L_7). **Pollen discarding** and **eaten pollen** are types of **active vectorial pollen loss**. Both result in loss of pollen from potential pollination, but because in one case pollen is being actively rejected while in the other case the pollen is being sought as a resource, the rates of loss and selective pressures resulting from the vectors' behaviors may differ.

Abiotic pollen losses (Fig. 2)—Categories of pollen losses from abiotic pollination systems mirror those in biotic systems. **Prepresentation pollinivory** (path 3a) or **postpresentation pollinivory** of pollen from anthers or cones generate **eaten pollen** (box L_1), while **postpresentation lack of collection** (path $3b_1$) leaves **remaining pollen** (box L_2). Pollen that is mechanically dislodged and lost by inanimate forces or passing animals seems no different to us in principle from losses that occur during normal transport in wind and water, and should be counted as **predeposition loss** (path 3c). Tremendous quantities of **misplaced pollen** (box L_3) can be lost from abiotic systems through **pollen misplacement**. Wind-dispersed pollen landing on inappropriate surfaces is frequent, as evidenced by the yellow film of conifer pollen that sometimes cover the surfaces of northern ponds or lakes.

Postdepositional losses (in biotic and abiotic systems)—Pollen often is deposited on many unfavorable stigmas: those that are nonconspecific, nonreceptive, or incompatible. Pollen (box L_8 in Fig. 1, box L_5 in Fig. 2) that lands on the stigma of a wrong species (**heterospecific pollen loss**) may not germinate or develop satisfactory pollen tubes. **Conspecific pollen loss** can occur through **unreceptive pollen deposition** when the stigma is unreceptive (boxes L_9 and L_6, **ill-times pollen**, for biotic and abiotic pollination, respectively) or via **incompatible pollen deposition** if the stigma is incompatible (boxes L_{10} and L_7, **incompatible pollen**; sporophytic incompatibility often takes place at the level of the stigma). If the ill-timing is because the unreceptive stigma is old, the loss is absolute; however, pollen on a stigma that is not receptive yet might still germinate if the stigma becomes receptive soon after deposition (e.g., in *Lithophragma parviflorum* (Saxifragaceae); O. Pellmyr, University of Cincinnati, Cincinnati, OH, personal communication). Similarly, incompatibility may fluctuate according to local ambient (e.g., temperature) conditions or there may be strict genetic determinism. Finally, a source of **postdeposition pollen loss** is pollen eaten off a stigma (box L_{11} in Fig. 1, box L_8 in Fig. 2, **eaten pollen**) by subsequent visitors foraging for stigmatic secretions or pollen.

After pollen is deposited on a stigma, further losses occur during the postpollination process of germination and fertilization. Pollen tubes could potentially be outcompeted by other pollen tubes (**outcompeted pollen tubes**, path 3f to box L_{12}, and path 3e to box L_9, for biotic and abiotic pollen, respectively). Incompatibility, path 3e to box L_{10}, can also result in postgermination losses in the style (e.g., gametophytic incompatibility mechanisms, which typically occur in the style). In some heterostylous systems, such as *Eichhornia paniculata* (Barrett, 1988), and distylous systems, such as *Amsinckia grandiflora* (Weller and Ornduff, 1989) where a cryptic incompatibility system exists (i.e., self-pollen tubes grow more slowly than outcross-pollen tubes), box S_2 could encompass the category of **illegitimate pollination** (Darwin, 1877a), i.e., transfer of pollen between improper height classes of stigma and anther (di- or tristylous). Even in postfertilization the resulting seed may be aborted individually or as part of an aborted fruit (path 10, **seed abortion**, to box L_{14}, **aborted seed**, or path 10, **fruit abortion**, to box L_{15}, **aborted fruit**). Such abortions of seeds and fruits are known to result from resource-related, genetic, or environmental factors (Stephenson, 1981).

Additional opportunities for **postdepositional pollen loss** in biotic-vectored systems (but unlikely in abiotic systems) are those on path 3d, resulting from **secondary pollen placement** (or **collection**). Secondary pollen loads can suffer the same losses as pollen on path 3c, and pollen on the second stigma could still suffer (via path 3e) the same postdeposition consequences detailed above.

VI. Common ratios of pollen quantities—In addition to the names for the quantities of pollen, ratios of these quantities are important measures of pollination biology for many investigators; indeed the confused popularity of the phrase "pollination efficiency" indicates their importance. Table 3 summarizes many ratios for both biotic and abiotic pollination systems; we list these ratios as systematically as possible following the order of quantities as shown (from left to right) in the figures. Many of these ratios can be further refined; for example, in animal-mediated pollination (Fig. 1) most can be measured per-visit, and in other cases a level (e.g., per-stigma, per-gynoecium) can be specified. The ratios for abiotic pollination systems (Fig. 2) are identical in concept but fewer in number than those identified for biotic systems. "Efficiency" here refers only to proportions or amounts of pollen transferred at each stage and not to any other costs of pollen transfer (rewards, attractants, etc.).

1. Denominator: **Pollen output at source**
   Numerator: **Vector pollen load**

The amount of pollen transferred to a vector is some fraction of the **pollen output** at the **source**. When viewed from the pollen donor's perspective this ratio is called **placement efficiency**; from the foraging vector's perspective it is called **collection efficiency**. When the denominator is **total pollen output** (P_T), then the ratio is **total placement efficiency** (or **total collection efficiency**); the analogous term **available placement efficiency** uses the denominator **available pollen output** (P_A). The ratio of the amount of pollen positioned on the vector for effective subsequent transfer to stigmas relative to pollen output is called **effective placement** (or **collection**) **efficiency**.

Numerator: **Stigma pollen load**

From the perspective of the **pollen donor**, pollen produced at the **source** has two aspects of success: a) dispersing to as many **pollen recipients** as possible; and b) placing an optimal number of pollen grains on each stigma. In the first case, **pollen dispersal**, the number of different receptive, conspecific, compatible stigmas (at several levels: gynoecia, inflorescences, ramets, and genets) on which pollen from a given **source** is deposited relative to the number of pollen grains at the **source** is called **dispersal efficiency**. Dispersal efficiency can be refined according to the Recipient level of the numerator (S_1–S_5). In the second case the amount of pollen deposited on a particular receptive, conspecific, compatible stigma (S_2) relative to the **pollen output** at the **source** is called **source efficiency**, with the usual qualifiers of **total** (S/P_T) and **available** (S/P_A) according to the denominator.

Numerators: **Successful pollen**, **seeds**

From the **pollen donor**'s point of view, the ratio of **fertilized ovules** (equivalent to F) relative to **pollen output** is called **fertilization efficiency**, a potentially important component of paternal fitness. As usual, the denominator can be either P_T or P_A with appropriate qualifiers **total** and **available**, respectively; the level (P_1–P_4) should be made clear. A second and even more critical measure of paternal fitness is the **seed set** (W) fathered by the pollen from a particular **source**; hence the ratio T_1/P that we call **siring efficiency**, with the analogous qualifiers **total** (P_T) and **available** (P_A) in the denominator. The difference between **fertilization efficiency** and **siring efficiency** depends on the extent of seed abortion during sporophytic development.

Numerator: **Pollen losses**

Pollen that is lost from the pollination process by any means (L_1 through L_{14}) could be measured relative to the amount of **pollen output** as a **pollen loss ratio**, L/P. The level at which pollen production is being considered should be specified (e.g., anther, flower, inflorescence). The agent of the pollen loss could also be used to classify the ratio (e.g., **pollen loss ratio from pollinivory**, . . . **from unreceptivity**, . . . **from pollen tube competition**, etc.), which can be calculated using **total** or **available pollen**.

2. Denominator: **Vector pollen load**

Numerator: **Stigma pollen load**

Vector pollinating efficiency, S/V is the amount of pollen deposited on a receptive, conspecific, compatible stigma relative to the **vector pollen load**; the denominator of this ratio could be either **total vector pollen load** or the **effective pollen load**. **Vector fertilization efficiency**, F/V, **vector seed set efficiency**, T_1/V, and **vector fruit set efficiency**, T_2/V are all potential measures of how effective a pollinator is at facilitating seed production in a plant species. Although the latter two are probably easier to measure, they may be affected by ambient environmental variables such as resource availability and climate; hence caution is required in interpreting these measures as strictly paternal traits.

The numerator and the denominator could be inverted when the pollen transfer is reversed. Deposited pollen can be picked up from a stigma by another vector, and retransported and deposited on a second stigma. The amount of pollen transferred from stigma to vector (**secondary vector pollen load**) relative to the **stigma pollen load** is denoted by the ratio V''/S and is called **secondary transfer efficiency**. When a secondary pollen load is redeposited on a new stigma as a **secondary stigma pollen load**, the efficiency of the transfer from vector to secondary stigma, S''/V'' is **secondary vector efficiency**.

3. Denominator: **Number of ovules**

Numerators: **Stigma pollen load**, **fertilized ovules**, **seeds**, **pollen ouput**

From the **pollen recipient**'s point of view at least three ratios with the number of ovules in the denominator can be important components of maternal fitness. The first measure, which is often useful as an indicator of pollen limitation to seed set, is the number of conspecific pollen grains deposited per ovule, S/# ovules, or **stigma pollen-ovule ratio**. The second is the ratio of fertilized ovules to total ovules, **ovule fertilization efficiency**. A third is the ratio of **seed set** to the total ovules, **ovule seed set efficiency**. A related and popular measure is Cruden's (1977) **pollen-ovule ratio**, P_2/# ovules (both terms measured within a flower as **source** and **recipient** simultaneously).

4. Denominator: **Stigma pollen load**

Numerators: **Germinated pollen load**, **seeds**, and **fruits**

Because the gynoecium exerts substantial control over pollen germination, pollen tube growth, fertilization, and seed development, ratios with **stigma pollen load** in the denominator may also serve as measures of maternal influences. The ratio of germinated pollen grains to the **stigma pollen load** is **germination efficiency**. Similarly, the number of fertilized ovules divided by the number of pollen grains in the **stigma pollen load** is called **stigma fertilization efficiency**. Analogously, there are **stigma seed set efficiency** and **stigma fruit set efficiency**.

5. Denominator: **Fertilized ovules**, **seeds**, and **fruits**

Numerators: **Aborted seeds** and **aborted fruits**

Two important ratios related to abortion of seeds or fruits are the **seed abortion rate** (L_{14}/T_1 per time) and the **fruit abortion rate** (L_{15}/T_2 per time); these could be measured relative to a single flower, an inflorescence, or a whole plant.

DISCUSSION

Let us now return to an example with which this paper began, the term "pollination efficiency," and examine terms that might be used instead to represent the concepts the different authors had in mind. Levin and Berube's (1972) use of the term included both what we call **vector efficiency** as well as **germination success** and calculations of **vector-induced pollen loss**. Kendall and Smith's (1975,

1976) measure of pods and beans produced per visit and Schemske and Horvitz's (1984) measure of fruit set per visit would be called **seed set per visit** or **fruit set per visit**. Parker's (1981, 1982) reference to the number of seeds that result from the visit by a single pollinator to an onion or sunflower inflorescence that is bagged before and after the visit and only exposed when receptive would also be called **seed set per visit**, as would Tepedino's (1981) measure of fruit and/or seed set per flower visit. Jennersten's (1984) reference to pollination efficiency is probably best represented by **vector pollen load**. If one assumes that touching a stigma can be equated with pollen deposition, then Dafni, Eisikowitch, and Ivri's (1987) measure of pollination efficiency can instead be measured as the equivalent of **stigma pollen load per visit**. Their other measure of "% pollinated stigmata" was assumed to be equivalent to **fruit set** (an assumption that would not hold for many plants). Richards (1987) equated pollinator efficiency with foraging rate, or the time that it took a pollinator or flower visitor (e.g., nectar robber) to visit ten to 50 flowers; we suggest the term **foraging rate** as an alternative. Schemske and Horvitz's (1984) measure of visitation frequency might incorporate the effects of **foraging rate**, but is not explicitly included in our lexicon. Their other estimates of pollination efficiency, trip efficiency per visit, and fruit-set efficiency of tripped flowers are not redefined by our lexicon. Andersson's (1988, p. 62) use of pollination efficiency also falls outside of our lexicon; his measure of inflorescence size could more properly be referred to in terms of an optimal size. Galen and Newport's (1987) and Waser and Price's (1990) measure of the amount of pollen transferred to a stigma by a single visit becomes **stigma pollen load per visit** in our terminology. Cruden et al.'s (1990) index of pollen grains deposited per stigma, divided by the number produced by the flower, is **total source efficiency**. Guo et al. (1990) measured **germination number** qualitatively (presence or absence of germinated pollen grains). Macfarlane, van den Ende, and Griffin's (1991) use of the term is outside of the lexicon we propose, and could probably be reported instead as an aspect of foraging behavior. Velthuis and Cobb (1991) don't explain what they actually meant by the term so we can't propose an alternative. Van Praagh and Hauschildt (1991) could have termed their measure more simply "fruit set per 100 flowers."

Our terminology also helps to clarify ambiguous use of the term "pollinator effectiveness." The variety of indices that Young (1988) described include **vector pollen load per source visit**, **stigma pollen load per visit**, and **seed set per visit**. Motten (1986) measured what we call **seed set per visit**, **fruit set per visit**, and a measure intermediate between **germinated pollen load per visit** and **successful pollen per visit**. Neff and Simpson (1990) basically measured **stigma pollen load per visit**, although they only observed presence/absence rather than a quantitative measure, and made their observations at the level of a composite flower head. Macfarlane, von den Ende, and Griffin's (1991) use doesn't conform to any of our suggestions here, while Galen and Newport's (1987) measure comprises both visitation rate and **stigma pollen load per visit**. Fenster's (1991) index is **stigma pollen load** and a measure of potential visitation rate. Which of these indices is most easily measured or most appropriate for consideration will depend on the particular system under study and the questions being asked.

Because the previous use of "pollination efficiency" and "pollinator effectiveness" has been so varied and ambiguous, we have not included these terms in our lexicon, and suggest that instead more specific terms be used to replace them in the future.

We hope that the path diagrams in Figs. 1 and 2 will provide a framework not only for understanding the variety of steps involved in pollination and their ecological significance, but also for asking questions about the evolution of pollination and plant breeding systems. For example, questions about the adaptive significance of changes in old pathways or the evolution of new ones may be quantified. In addition, the evolution of breeding systems and floral morphology in general may be more easily understood in light of the minimization of specific loss functions or increased efficiency of successful pollen transfer.

We will consider this paper successful if it eliminates the confusion about the concepts and definitions of these terms, and if it stimulates additional research into some of the pathways that we have described that have not yet been well studied. We found that the figures and tables helped us to identify pathways that weren't obvious before, and to clarify important parameters to measure in each of these scenarios. We hope that this lexicon and the figures will guide logical, empirical, and experimental examination of potential pathways and their evolutionary constraints. We expect further refinement of this lexicon will be necessary as our understanding of pollination biology and its intricacies improves.

LITERATURE CITED

AKER, C. L., AND D. UDOVIC. 1981. Oviposition and pollination behavior of the yucca moth, *Tegeticula maculata* (Lepidoptera: Prodoxidae), and its relation to the reproductive biology of *Yucca whipplei* (Agavaceae). *Oecologia* 49: 96–101.

ANDERSSON, S. 1988. Size-dependent pollination efficiency in *Anchusa officinalis* (Boraginaceae): causes and consequences. *Oecologia* 76: 125–130.

BARRETT, S. C. H. 1988. Evolution of breeding systems in *Eichhornia* (Pontederiaceae): a review. *Annals of the Missouri Botanical Garden* 75: 741–760.

BUCHMANN, S. L. 1983. Buzz pollination in angiosperms. *In* C. E. Jones and R. J. Little [eds.], Handbook of experimental pollination biology, 73–113. Scientific and Academic Editions, New York, NY.

CRUDEN, R. W. 1973. Reproductive biology of weedy and cultivated *Mirabilis* (Nyctaginaceae). *American Journal of Botany* 60: 802–809.

———. 1977. Pollen-ovule ratios: a conservative indicator of breeding systems in flowering plants. *Evolution* 31: 32–46.

———, K. K. BAKER, T. E. CULLINAN, K. A. DISBROW, K. L. DOUGLAS, J. D. ERB, K. J. KIRSTEN, M. L. MALIK, E. A. TURNER, J. A. WEIER, AND S. R. WILMOT. 1990. The mating system and pollination biology of three species of *Verbena* (Verbenaceae). *Journal of the Iowa Academy of Science* 97: 178–183.

DAFNI, A., D. EISIKOWITCH, AND Y. IVRI. 1987. Nectar flow and pollinators' efficiency in two co-occurring species of *Capparis* (Capparidaceae) in Israel. *Plant Systematics and Evolution* 157: 181–186.

DARWIN, C. R. 1877a. The different forms of flowers on plants of the same species. Reprinted. The University of Chicago Press, Chicago, IL.

———. 1877b. The various contrivances by which orchids are fertilised by insects, 2d ed. Reprinted. The University of Chicago Press, Chicago, IL.

DOLE, J. A. 1990. Role of corolla abscission in delayed self-pollination of *Mimulus guttatus* (Scrophulariaceae). *American Journal of Botany* 77: 1505–1507.

———. 1992. Reproductive assurance mechanisms in three taxa of the *Mimulus guttatus* complex (Scrophulariaceae). *American Journal of Botany* 79: 650–659.

FAEGRI, K., AND L. VAN DER PIJL. 1979. The principles of pollination biology, 3d ed. Pergamon Press, Oxford.

FENSTER, C. B. 1991. Gene flow in *Chamaecrista fasciculata* (Leguminosae). I. Gene dispersal. *Evolution* 45: 398–409.

FREE, J. B. 1966. The pollinating efficiency of honey-bee visits to apple flowers. *Journal of Horticultural Science* 41: 91–94.

GALEN, C., AND M. E. A. NEWPORT. 1987. Bumble bee behavior and selection on flower size in the sky pilot, *Polemonium viscosum. Oecologia* 74: 20–23.

GALIL, J. 1973. Topocentric and ethodynamic pollination. *In* N. B. M. Brantjes and H. F. Linskens [eds.], Pollination and dispersal, 85–100. Proceedings of a symposium, published by the Department of Botany, University of Nijmegen, Netherlands.

GILL, D. E. 1989. Fruiting failure, pollinator inefficiency, and speciation in orchids. *In* D. Otte and J. Endler [eds.], Speciation and its consequences, 458–481. Sinauer, Sunderland, MA.

GUO, Y.-H., R. SPERRY, C. D. K. COOK, AND P. A. COX. 1990. The pollination ecology of *Zannichellia palustris* L. (Zannichelliaceae). *Aquatic Botany* 38: 341–356.

HARDER, L. D., AND J. D. THOMSON. 1989. Evolutionary options for maximizing pollen dispersal of animal-pollinated plants. *American Naturalist* 133: 323–344.

INOUYE, D. W. 1980. The terminology of floral larceny. *Ecology* 61: 1251–1253.

JENNERSTEN, O. 1984. Flower visitation and pollination efficiency of some North European butterflies. *Oecologia* 63: 80–89.

KEARNS, C. A., AND D. W. INOUYE. 1993. Techniques for pollination biologists. University Press of Colorado, Niwot, CO.

KENDALL, D. A., AND B. D. SMITH. 1975. The pollinating efficiency of honeybee and bumblebee visits to field bean flowers (*Vicia faba* L.). *Journal of Applied Ecology* 12: 709–717.

———, AND ———. 1976. The pollinating efficiency of honeybee and bumblebee visits to flowers of the runner bean *Phaseolus coccineus* L. *Journal of Applied Ecology* 13: 749–752.

KENNEDY, H. 1973. Notes on Central American Marantaceae. I. New species and records from Panamá and Costa Rica. *Annals of the Missouri Botanical Garden* 60: 413–426.

LEVIN, D. A., AND D. E. BERUBE. 1972. *Phlox* and *Colias*: the efficiency of a pollination system. *Evolution* 26: 242–250.

LLOYD, D. G. 1979. Some reproductive factors affecting the evolution of self-fertilization in plants. *American Naturalist* 113: 67–79.

MACFARLANE, R. P., H. J. VAN DEN ENDE, AND R. P. GRIFFIN. 1991. Pollination needs of 'grasslands pawera' red clover. *Acta Horticulturae* 288: 399–403.

MACIOR, L. W. 1968. Pollination adaptation in *Pedicularis groenlandica. American Journal of Botany* 55: 927–932.

MONTALVO, A. M. 1992. Relative success of self and outcross pollen comparing mixed- and single-donor pollination in *Aquilegia caerulea. Evolution* 46: 1181–1198.

MOTTEN, A. F. 1986. Pollination ecology of the spring wildflower community of a temperate deciduous forest. *Ecological Monographs* 56: 21–42.

NEFF, J. L., AND B. B. SIMPSON. 1990. The roles of phenology and reward structure in the pollination biology of wild sunflower (*Helianthus annuus* L., Asteraceae). *Israel Journal of Botany* 39: 197–216.

NILSSON, L. A., E. RABAKONANDRIANINA, B. PETTERSSON, AND J. RANAIVO. 1990. "Ixoroid" secondary pollen presentation and pollination by small moths in the Malagasy treelet *Ixora platythyrsa* (Rubiaceae). *Plant Systematics and Evolution* 170: 161–175.

PARKER, F. D. 1981. How efficient are bees in pollinating sunflowers? *Journal of the Kansas Entomological Society* 54: 61–67.

———. 1982. Efficiency of bees pollinating onion flowers. *Journal of the Kansas Entomological Society* 55: 171–176.

POWELL, J. A. 1992. Interrelationships of yuccas and yucca moths. *Trends in Ecology and Evolution* 7: 10–15.

RICHARDS, K. W. 1987. Diversity, density, efficiency, and effectiveness of pollinators of cicer milkvetch, *Astragalus cicer* L. *Canadian Journal of Zoology* 65: 2168–2176.

SCHEMSKE, D. W., AND C. B. FENSTER. 1983. Pollen-grain interactions in a neotropical *Costus*: effects of clump size and competitors. *In* D. L. Mulcahy and E. Ottaviano [eds.], Pollen: biology and implications for plant breeding, 405–410. Elsevier Science, New York, NY.

———, AND C. C. HORVITZ. 1984. Variation among floral visitors in pollination ability: a precondition for mutualism specialization. *Science* 225: 519–521.

SIMBERLOFF, D., AND T. DAYAN. 1991. The guild concept and the structure of ecological communities. *Annual Review of Ecology and Systematics* 22: 115–143.

SNOW, A. 1982. Pollination intensity and potential seed set *Passiflora vitifolia. Oecologia* 55: 231–237.

SPEARS, E. E., JR. 1983. A direct measure of pollinator effectiveness. *Oecologia* 57: 196–199.

STEPHENSON, A. G. 1981. Flower and fruit abortion: proximate causes and ultimate function. *Annual Review of Ecology and Systematics* 12: 253–281.

SVENSSON, L. 1986. Secondary pollen carryover by ants in a natural population of *Scleranthus perennis* (Caryophyllaceae). *Oecologia* 70: 631–632.

TEPEDINO, V. J. 1981. The pollination efficiency of the squash bee (*Peponapis pruinosa*) and the honey bee (*Apis mellifera*) on summer squash (*Cucurbita pepo*). *Journal of the Kansas Entomological Society* 54: 359–377.

THOMSON, J. D., AND B. A. THOMSON. 1992. Pollen presentation and viability schedules and their consequences for reproductive success through animal pollination. *In* R. Wyatt [ed.], Ecology and evolution of plant reproduction: new approaches, 1–24. Chapman and Hall, New York, NY.

VAN PRAAGH, G. P., AND H. HAUSCHILDT. 1991. Evaluation of shoot-bending, pruning and pollination for increasing fruit-set and yield on young "Cox" trees. *Acta Horticulturae* (Proceedings of the Sixth International Symposium on Pollination, Tilburg, the Netherlands) 288: 244–248.

VAUGHTON, G., AND M. RAMSEY. 1991. Floral biology and inefficient pollen removal. *Australian Journal of Botany* 39: 167–177.

VELTHUIS, H. H. W., AND L. COBB. 1991. Pollination of *Primula* in a greenhouse using bumblebees. *Acta Horticulturae* (Proceedings of the Sixth International Symposium on Pollination, Tilburg, the Netherlands) 288: 199–203.

WASER, N. M., AND M. V. PRICE. 1990. Pollination efficiency and effectiveness of bumble bees and hummingbirds visiting *Delphinium nelsonii. Collectanea Botanica* (Barcelona) 19: 9–20.

WEBB, C. J., AND D. G. LLOYD. 1986. The avoidance of interference between the presentation of pollen and stigmas in angiosperms II. Herkogamy. *New Zealand Journal of Botany* 24: 163–178.

WELLER, S. G., AND R. ORNDUFF. 1989. Incompatibility in *Amsinckia grandiflora* (Boraginaceae): distribution of callose plugs and pollen tubes following inter- and intramorph crosses. *American Journal of Botany* 76: 277–282.

WIEBES, J. T. 1979. Co-evolution of figs and their insect pollinators. *Annual Review of Ecology and Systematics* 10: 1–12.

YEO, P. F. 1993. Secondary pollen presentation. Form, function and evolution. Springer Verlag, New York, NY.

YOUNG, H. J. 1988. Differential importance of beetle species pollinating *Dieffenbachia longispatha* (Araceae). *Ecology* 69: 832–844.

APPENDIX 1. GLOSSARY. Phrases and terms are listed alphabetically. Closely related definitions are grouped together under a major heading. Critical distinctions between similar terms are italicized for emphasis. Many of the terms used here implicitly refer to pollen as a resource but could also apply to other floral resources such as nectar, oils, and resins by substituting the appropriate qualifier. As in Table 3, definitions of ratios can be converted into related measures like "efficiency per visit," rates like "collection efficiency per day," or alternative levels like "pollen-ovule ratio per inflorescence."

Collection efficiency—The ratio of the number of pollen grains transferred to a biotic Vector relative to pollen produced or available elsewhere. Collection Efficiency is from the perspective of the pollinator in contrast to Placement Efficiency which is from the perspective of the Source Plant or Pollen Donor. Subcategories contrast Total (denominator is Total Source Pollen) vs. Available (denominator is Available Source Pollen), Active vs. Passive, Primary vs. Secondary, and Effective.

Active collection efficiency—The ratio of the number of pollen grains *actively gathered* by a flower visitor during Active Pollen Collection relative to either Available Source Pollen (Available Active Collection Efficiency) or Total Source Pollen (Total Active Collection Efficiency).

Passive collection efficiency—The ratio of the number of pollen grains *accumulated passively* by a flower visitor during a visit to a flower relative to either Available Source Pollen (Available Passive Collection Efficiency) or the Total Source Pollen (Total).

Primary collection efficiency—The ratio of the number of pollen grains collected from the *Source* relative to the Available Source Pollen.

Secondary collection efficiency—The ratio of the number of pollen grains (already deposited) picked up from a *stigma* by a flower visitor relative to the number of pollen grains on the stigma. Can be measured for either active or passive collection.

Effective collection efficiency—The ratio of the Effective Vector Pollen Load to Pollen Output.

Conspecific pollen loss—A subcategory of Postdeposition Pollen Loss.

Dislodged pollen—Pollen that is blown or washed off anthers before being transferred to a Vector, either by the activities of a flower visitor in Vector-induced Pollen Loss or by abiotic forces in Nonvector-induced Pollen Loss.

Dislodgement—The activity of a biotic or abiotic external agent, or visitor or actual pollinator that generates dislodged pollen.

Dispersal—The movement of pollen from Source to all points of Deposition.

Dispersal distance—The distance pollen is moved from Source to point of Deposition.

Dispersal efficiency—The ratio of the number of dispersal targets (stigmas, flowers, inflorescences, capitula, ramets, or genets) on which pollen from a given Source is placed relative to the number of pollen grains at the Source. See also Transfer Efficiency. This ratio could be calculated using Available Source Pollen (Available dispersal efficiency) or Total Source Pollen (Total dispersal efficiency) as the denominator. Two examples of recipient levels are:

Gynoecium dispersal efficiency—The ratio of the number of different gynoecia on which pollen from a Source is placed relative to the number of pollen grains at the Source.

Stigma dispersal efficiency—The ratio of the number of different stigmas (Dispersal Targets) on which pollen from a Source is placed relative to the number of pollen grains at the Source.

Dispersal target number—The number of different stigmas on which pollen from a single Source is Deposited.

Dispersal time—The time between pollen collection at the Source and Deposition on a stigma.

Eaten pollen—Pollen consumed as food by a flower visitor or its progeny.

Predispersal eaten pollen—Pollen that is eaten by a flower visitor while *at the Source* engaged in Predispersal Pollinivory.

Postcollection eaten pollen—Pollen eaten by a Vector during dispersal, *after collection* from the Source, by Predeposition Pollinivory. For example, the pollen groomed off its own body or retrieved from pollen baskets; also, the pollen fed to occupants in the visitor's nest.

Postdeposition eaten pollen—Pollen eaten from a *stigma* after it had previously been deposited by a pollinator.

Efficiency—Generally defined as output over input, and with a range from 0 to 1.0. In the context of pollination, we define efficiency as a quantity of pollen at a location downstream in the pollination process divided by a quantity upstream in the process. Qualifiers included here are Collection, Dispersal, Fertilization, Placement, Siring, Source, and Vector Efficiency (cf).

Fertilization efficiency—A subcategory of Source Efficiency.

Fruit set—The number of fruits produced as a consequence of the pollination process and subsequent fertilizations. A postpollination process.

Fruit set efficiency—The ratio of the number of fruits produced relative to the number of flowers under consideration.

Stigma fruit set efficiency—The ratio of the number of fruits produced relative to the number of pollen grains deposited on the stigma(s) of a flower.

Germination—The development of a pollen tube by a pollen grain (following deposition on a stigma).

Germination efficiency—The ratio of the number of germinated pollen grains to all pollen grains deposited on a stigma. Subcategories, which can be measured Per-visit, include Conspecific vs. Heterospecific, and Total (conspecific + heterospecific pollen).

Conspecific germination efficiency—The ratio of the number of *conspecific* germinated pollen grains relative to either just the *conspecific* pollen grains deposited on a stigma (Partial) or the Total Stigma Pollen Load (Total).

Heterospecific germination efficiency—The ratio of the number of heterospecific pollen grains that germinate relative to either just the *heterospecific* pollen grains deposited on a stigma (Partial) or the Total Stigma Pollen Load (Total).

Germination number—The subset of pollen grains deposited on stigmas that germinate. Can be specified as a Conspecific, Heterospecific, or Total Germination Number.

Threshold germination number—The *minimum number* of pollen grains required on a stigma for successful germination to occur.

Source-specific germination number—The number of germinated pollen grains in a Stigma Pollen Load that are derived from a single Source (the level must be specified; e.g., per anther or per flower).

Stigma germination number—The subset of all pollen grains deposited on a stigma that proceed to germinate.

Heterospecific pollen loss—A subcategory of Postdeposition Pollen Loss.

Illegitimate pollination—In distylous species, pollen deposition on a stigma of the same morph. In tristylous species, pollen deposited between two floral morphs with anthers at different levels.

Lost pollen—The pollen irretrievably eliminated from the pollination path from Source to Fertilization. See Pollen Loss.

Misplaced pollen—Pollen that is lost from abiotic dispersal by landing on an inappropriate surface (i.e., someplace other than a conspecific stigma). A subcategory of Postdeposition Pollen Loss.

Placement efficiency—The ratio of the number of pollen grains transferred to a Vector from a flower relative to the number of pollen grains at the Source (either Total or Available at the time of the visit). Placement Efficiency is the transfer from the perspective of the Source; it contrasts with Collection Efficiency which is the same ratio from the perspective of the pollinator. Subcategories contrast Total vs. Available, and Effective.

Effective placement efficiency—The ratio of the Effective Vector Pollen Load relative to either the Available Source Pollen or the Total Source Pollen.

Vector-species-specific placement efficiency—The cumulative number of pollen grains transferred to all the individuals of a *single species* of pollinator (or visitor) visiting a Source relative to either the Available Source Pollen or the Total Source Pollen.

Pollen acquisition—The receipt of pollen by a Stigma from a pollinator, from the plant's perspective. Contrast with Pollen Deposition, which is the same transfer from the pollinator's perspective.

Active pollen acquisition—The receipt of pollen by a stigma through some *mechanical motion* of the flower or its parts, such as a trip or spring.

Passive pollen acquisition—The receipt of pollen by a stigma when *no movement* of floral parts is involved; only the activities of the Vector are responsible.

Pollen collection—The gathering of pollen by a visitor from a Source. The transfer to the pollinator is from the Vector's perspective. Contrast with Pollen Placement which is the same transfer from the flower's perspective.

Active pollen collection—The gathering of pollen from a Source accomplished by a flower visitor's foraging behaviors, which are actively directed toward pollen as a resource.

Passive pollen collection—The adherence of pollen to a pollinator during a visit to a flower without directed pollen gathering behaviors by the Vector.

Primary collection—The *first* transfer of a pollen grain to the body of a Vector, from the Source of pollen production or presentation.

Secondary collection—The transfer of pollen that is already on a stigma from a previous Deposition back onto another Vector.

Pollen deposition—The transfer of pollen from Vector to Stigma from the perspective of the pollinator; Pollen Acquisition is the same transfer from the perspective of the plant or stigma. Subcategories include:

Active deposition—The intentional transfer of pollen onto a stigma by a pollinator (part of "ethodynamic pollination"). Currently known only in fig wasps and yucca moths.

Passive deposition—The unintentional or passive transfer of pollen from Vector to stigma during the course of a visit to a flower by a pollinator engaged in foraging for rewards such as nectar, pollen, or fragrances.

Primary deposition—The first time that a pollen grain contacts a stigma.

Secondary deposition—The second contact with a stigma that pollen grains experience when redeposited after a Secondary Collection and subsequent transport.

Pollen donor—A plant functioning as a male and a Source of pollen; could be specified at the level of theca, anther, pollinium, flower, inflorescence, ramet. Synonymous with Pollen Source.

Pollen load—The absolute quantity of pollen grains (mass or number) at a location in the pollination pathway. Two major sites of pollen loads are Vector and Recipient Pollen Loads.

Recipient pollen load—The quantity of pollen on the Pollen Recipient following Deposition. Can be measured at the level of capitulum, gynoecium, inflorescence, etc. Two examples are given here.

Capitulum pollen load—The number of pollen grains deposited on all of the stigmas of a composite flower head (e.g., Asteraceae); a specific case of Inflorescence Pollen Load.

Stigma pollen load—The number of pollen grains deposited on the complete stigma of a flower. In addition to the subcategories below, contrasts include Total vs. Per-visit, Conspecific vs. Heterospecific, and Compatible vs. Incompatible.

Primary stigma pollen load—The number of pollen grains on a stigma that have not been deposited previously on another stigma.

Secondary stigma pollen load—The number of pollen grains on a stigma derived from a Secondary Deposition; i.e., pollen that had been deposited once but collected secondarily by a subsequent visitor and *redeposited* on a stigma.

Stigma lobe pollen load—The number of pollen grains deposited on one lobe of a branched or multilobed stigma, such as in Gramineae and Gentianaceae.

Threshold pollen load—The minimum number of pollen grains required to accomplish fertilization of at least one ovule.

Vector pollen load—The amount of pollen or number of grains carried by a Vector during dispersal and before Deposition. Subcategories contrast Effective and Total:

Effective vector pollen load—The number of pollen grains positioned on the body of a Vector in a place that makes likely their deposition on a stigma. A subset of Total Vector Pollen Load; subcategories can include Primary vs. Secondary.

Total vector pollen load—The total number of pollen grains on the body of a pollinator irrespective of position and without regard to probability of successful deposition on a stigma. Subcategories include:

Primary vector pollen load—The number of pollen grains on the body of a pollinator that came directly from the *Source* of production.

Secondary vector pollen load—The number of pollen grains on a Vector that came from a *Stigma,* and hence had already been deposited once before.

Pollen loss—The terminal departure of pollen from the pollination pathway between Source and successful Fertilization. Subcategory contrasts include Active vs. Passive, Heterospecific vs. Conspecific, Predispersal vs. Predeposition vs. Postdeposition, Vector-induced vs. Nonvector-induced. See also Pollinivory.

Active pollen loss—Losses of pollen from the pollination pathway due to the actions of the Source, Vector, or Stigma themselves, such as explosive dehiscence, pollinivory, and germination inhibition.

Passive pollen loss—Losses of pollen from the pollination pathway due to external forces not under the control of the Source, Vector, or Stigma, such as abiotic and/or biotic disturbances.

Pre-dispersal pollen loss—The process of pollen loss at the Source *before* transfer to a Vector. Causes of the loss include pollinivory, failure to dehisce or otherwise not available for transfer, and dislodgement by visitors or external forces. See Dislodged Pollen and Misplaced Pollen.

Non-vector-induced pollen loss—The loss of dehisced pollen that is dislodged by abiotic disturbance, and is blown or washed away before being transferred to the potential Vector.

Pollen loss ratio—The number of pollen grains lost from the pollination process relative to the number of pollen grains at the Source. The location or process in the pathway where the pollen loss occurs must be specified, as should the Source level of pollen (e.g., anther, flower, inflorescence). The denominator must also be specified relative to Available Source Pollen (Available Pollen Loss Ratio) or Total Source Pollen (Total).

Vector-induced pollen loss—Pollen that is dislodged and lost from the pollination process due to the activities of a flower visitor. The quantity of pollen lost is Vector-induced Lost Pollen.

Pre-deposition pollen loss—The loss of pollen *during* transport by a biotic or abiotic Vector.

Active vectorial pollen loss—Loss of pollen from the body of a Vector as a consequence of directed behaviors of the Vector itself, such as self-grooming or consumption. The quantity of pollen lost is Active Vectorial Lost Pollen. Subcategories include Pollen Discarding and Predeposition Pollinivory.

Pollen discarding—The rejection of pollen by Vectors from their bodies in the process of self-grooming or mutual-grooming by nest mates or at the time of consumption because of detected unpalatability.

Predeposition pollinivory—see Pollinivory.

Passive vectorial pollen loss—The process of pollen loss from the body of a Vector generated by external friction or shear forces such as brushed surfaces or wind, not by directed behaviors of the Vector itself. The quantity of pollen lost is Passive Vectorial Lost Pollen.

Postdeposition pollen loss—The loss of pollen from the pollination process after deposition on a Stigma. Causes of the loss include failure to germinate because of heterospecificity, incompatibility, pollinivory, and competition. See also Misplaced Pollen.

Conspecific pollen loss—Failure of pollen that had been acquired by a conspecific stigma to germinate or succeed in fertilization. Causes of germination failure include incompatibility and pollinivory. Failure of germinating male gametophytes to fertilize ovules may be due to incompatibility of pollen tubes with style or pollen tube competition. Subcategories include Pollinivory (cf.), Ill-timed, and Incompatible.

Ill-timed pollen loss—The loss of pollen because of deposition on a stigma before or after its period of receptivity.

Incompatible pollen loss—The loss of pollen because of deposition on a genetically incompatible, conspecific stigma.

Heterospecific pollen loss—The loss of pollen that is deposited on the stigma of a nonconspecific species of plant. Often such pollen will not germinate or will fail to fertilize the heterospecific ovules.

Pollen output—The pollen produced by a production unit at the Source. Subcategories include the hierarchical levels or locations of pollen production, i.e., theca, anther, pollinium, flower, inflorescence, ramet.

Available pollen output—The portion of the total amount of pollen produced that is available for dispersal at an instant in time.

Total pollen output—All of the pollen grains produced at the Source. The level can be specified, e.g., theca, anther, pollinium, flower, inflorescence, or ramet.

Pollen-ovule ratio—The ratio of the number of pollen grains produced by a flower relative to the number of ovules produced by the *same* flower. Contrast with Stigma Pollen-Ovule Ratio.

Pollen placement—The transfer of pollen (or a pollinium) from Source to Vector from the plant's perspective. Contrast with Pollen Collection, which is the same transfer from the Vector's perspective.

Active pollen placement—The transfer of pollen (or pollinium) to a pollinator as it visits a flower, through some active mechanism by flower parts, such as a trip or spring mechanism.

Passive pollen placement—The transfer of pollen to a flower visitor as it visits a flower to collect a resource such as nectar, pollen, or fragrance, without any movement on the part of the plant.

Secondary pollen placement—The transfer of pollen, previously transferred from a stigma to a Vector, back onto another stigma.

Pollen recipient—A plant functioning as a female and acquiring pollen from a Vector. The level (stigma, gynoecium, flower, ramet) should be specified.

Pollen source—The site of pollen production, packaging and presentation. Can be specified at the level of theca, anther, pollinium, flower, inflorescence, or ramet. Synonymous with Pollen Donor.

Pollen tube—The structure generated by a germinating male gametophyte through a style from stigma to ovary that allows pollen nuclei to migrate down the style to effect fertilization. In the present context of pollination biology, subcategory contrasts include:

Outcompeted pollen tube—A pollen tube (male gametophyte) that is unsuccessful in fertilizing an ovule because it fails to reach the ovary before a successful tube.

Successful pollen tube—The pollen tube (male gametophyte) that reaches the ovule first and is responsible for the double fertilization.

Pollination—The umbrella word that comprises the first three phases of sexual reproduction in flowering plants: 1) Production, presentation, and transfer of pollen at a Source; 2) Transport of pollen by a Vector; and 3) Deposition of pollen onto a stigma. Equivalent expressions are (a) pollen output + pollen placement and dispersal + pollen acquisition (from the perspective of the plants), or (b) pollen output + pollen collection and dispersal + pollen deposition (from the point of view of the pollinator). Germination of pollen grains into pollen tubes, double fertilizations, and ensuing seed and fruit development are *postpollination processes.*

Pollinivory—The consumption of pollen as food by an animal.

Postdepositional pollinivory—The consumption of pollen after it has been deposited on a stigma.

Predeposition pollinivory—The consumption of pollen by a Vector *after* the pollen has been collected from the source. Typically the pollen is groomed off the body of the Vector and eaten directly or carried to the nest and eaten. Distinct from Predispersal Pollinivory.

Predispersal pollinivory—Consumption of pollen as food by an animal (often an effective pollinator) at the Source at the time of a visit.

Pollen presentation—The positioning of ripe or dehisced pollen at the Source in a way that enhances the transfer to a Vector. Subcategories include:

Primary pollen presentation—The position of presentation is at the original site of production, namely the anther or thecae of anthers.

Secondary pollen presentation—"The presentation of pollen either in floral structures other than the anther-sacs (thecae) in which it is produced or by special mechanisms of expulsion involving contact of the pollen with other floral parts" (Yeo, 1993).

Remaining pollen—Pollen that is not removed or dispersed from the Source. In biotic pollination this may occur because the flower was never effectively visited.

Secondary pollen placement—The transfer of pollen from a Stigma to a Vector after it had already been deposited on a Stigma.

Secondary pollen transfer—The transfer of pollen that was released from an anther (either accidentally or adaptively) and landed on another part of the flower, onto a vector.

Seed set—The number of viable seeds produced (postpollination). The levels of the recipient (carpel, flower, inflorescence, ramet, etc.) should be specified.

Seed set probability—The ratio of the number of viable seeds to the number of ovules; can be measured at levels such as flower, capitulum, inflorescence.

Siring efficiency—A subcategory listed under Source efficiency.

Source efficiency—The ratio of the number of pollen grains deposited on a conspecific stigma relative to the Output at the pollen Source. Subcategories include Available (denominator is Available Source Pollen), vs. Total (denominator is Total Source Pollen).

Fertilization efficiency—The ratio of the number of pollen grains that succeed in fertilizing ovules relative to either Available Source Pollen (Available Fertilization Efficiency) or Total Source Pollen (Total). Differs from Siring Efficiency by having *fertilized ovules* in the numerator rather than *seeds.*

Siring efficiency—The ratio of the number of viable seeds produced by pollen from a single Source relative to either Available Source Pollen (Available Siring Efficiency) or Total Source Pollen (Total Siring Efficiency). Differs from Fertilization Efficiency by the amount of seed abortion that occurs between fertilization and seed set.

Stigma load evenness—A measure of variation in the distribution of stigma pollen loads on all targets hit by a single pollen Source.

Stigma load evenness efficiency—The evenness of stigma pollen loads on all targets hit by a single pollen Source relative to the size of the Pollen Output of that Source.

Stigma pollen-ovule ratio—The ratio of the number of conspecific pollen grains deposited on a receptive conspecific stigma relative to the number of ovules the flower has. Contrast with Pollen-ovule Ratio.

Stigma efficiency—The ratio of viable seeds and fruits produced relative to Stigma Pollen Loads.

Stigma fertilization efficiency—The ratio of the number of pollen tubes that succeed in *fertilizing ovules* relative to the number of pollen grains deposited on the stigma (Stigma Pollen Load). Can be measured per-visit.

Stigma seed set efficiency—The ratio of the number of seeds produced relative to the number of pollen grains deposited on the stigma (Stigma Pollen Load). Can be measured per-visit.

Vector efficiency—The ratio of the number of pollen grains deposited on a conspecific stigma relative to the amount of pollen on the pollinator. Subcategories contrast Primary vs. Secondary, Effective vs. Total Vector Efficiency.

Effective vector efficiency—The ratio of the number of pollen grains deposited on a stigma relative to the Effective Vector Pollen Load.

Primary vector efficiency—The ratio of the number of pollen grains from a Primary Vector Pollen Load deposited for the first time on a stigma relative to the Total Vector Pollen Load.

Secondary vector efficiency—The ratio of the number of pollen grains from a Secondary Vector Pollen Load that are redeposited on a stigma relative to the number in the Secondary Vector Pollen Load.

Total vector efficiency—The ratio of the number of pollen grains deposited on a stigma relative to the Total Vector Pollen Load.

Vectorial pollen loss—Synonym for Predeposition Pollen Loss. Pollen lost from the pollination process after being transferred from Source to Vector but before Deposition.