ANGIOSPERM POLLINATION AND SEED DISPERAL, A REVIEW

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INTRODUCTION

The aim of this review is to provide a summary conceptual and methodological framework in studies of Angiosperm pollination and seed dispersal conducted in tropical forest canopies. We review briefly descriptive, and eventually compare protocols designed to examine environmental and microenvironmental parameters, life and growth forms, morphology and other ornamental or protective characters (color, odor, texture, chemical composition), spatial and temporal distribution patterns, average abundance, visitor activity and flux, and the effectiveness of pollinators and seed dispersal. Particular emphasis is given to methods adopted in tropical forest canopies research, notably developed or modified from ground-level techniques. Plants and traits characteristics involved in pollination or seed dispersal processes are considered in biogeographical terms related to investments, reward, and selection. Methodological techniques dedicated to Angiosperm and frugivore reproduction. Practical suggestions for common database implementations are made, together with a presentation of existing and new standardised

POLLINATION

Besides single配偶 climbing techniques (Perry 1978; Perry & Williams 1981, Mitchell 1982, Dietrich & Nil 1993) a set of different canopy access methods like macaques and canopies, canopy walkways (Brown et al. 1995, campo, Dietrich & Nil 1993), balloons (Halka & Gallandt 1990, Halka & Pascal 1992, Halka 1998), and gorila systems (Gortlerer & Diring 1999) have been developed to enhance canopy access. For more complete information on common protocols in pollination ecology there are Dahl's practical approach in Pollination Ecology and Keams & Stowe's Techniques for Pollination Biology. For references on reproductive biology and genetics of non-tropical canopies, see Murawski (1995), and for progress in pollination ecology in recent years see Gortlerer (1985, 1989, 1993, 1996). Each form of flowers or blossoms (sense Fregi & van der Pijl 1979) can have a special role in pollination and fruit production and dispersal of pollen and seeds. An understanding of floral structures, their characteristics, and their function is fundamental for any pollination study. We can distinguish between
flower types and pollination syndromes. Flower types are categories of similar flowers based on morphological and physico-chemical characters (stem, color, oil, nectar, etc.), and pollination syndromes are the patterns of these characters and their correlation with interacting pollinating agents. Several of these characters are easily detectable and investigated in the field under canopy conditions.

Pollination is an important step in the life history of many tropical forest trees and epiphytes, because non-pioneer forest trees commonly do not produce masses and both trees and epiphytes rely on seed production to reach safe sites for germination. However, pollination should be studied in the context of species life history (see Fig. 1), which is frequently unknown for tropical forest species (Stevens 1991, Clark & Clark 1992).


**Fig. 1.** Important steps in canopy plant life cycles. Key factors of the ecology of tropical forest canopies are the allocation of resources to flowers, fruitlets, and seeds versus vegetative growth and the interaction with animal vectors in pollination and seed dispersal.

78
Flower colors. Flower colors may be the most obvious characters in advertisement for pollinators but they are effective together with other stimuli like odour, size, shape, etc. Hence they should be tested as part of a broader advertisement context. Flower color has been analysed with respect to community species, taxonomic species, specific pollinators, flower lifetime changes, and intraspecific variability. Flower colors affect and guide pollinators (Waser & Price 1981, Kven 1983) and signal pollen or nectar availability or location (Gori 1983, 1989; Wcislo 1991).

Because of interpretation difficulties, objective methods of color measurement should be used. Human visual evaluation, photography using different filters, video cameras, and colorimetric measurements with spectrophotometers have been used. See Dafni (1992) for a detailed description and comparison of methods, and for additional references for widespread reflectance patterns, see Willmer & Garbett (1981, 1989), Bed et al. (1985), Mace & Rees (1986), Inouye & Pyke (1988), Memel (1990), and Memel & Backhaus (1991).

Flower adornments. Fragrances may be as important in colour in admiring for pollinators. Special scent glands (ostioles) have been discovered (Vogel 1940) but most flowers show a diffuse production of scents and produce several different compounds. See Dafni (1994) for an overview of floral volatiles in insect biology.

Several techniques have been used to study the effect of scents on potential pollinators (see Dafni 1992). Some of them are for experimental situations and not applicable in canopy research. For localization of pollinators, see Vogel (1963, 1990). For rapid descriptions of large numbers of species in the field and identification of the pollination syndrome it may be sufficient to use the human nose for detection of floral scents. Recently, small devices for scent collection in the field have been developed, which allow analysis of the chemical compounds by gas chroma- tography and mass spectrometry (Nillson 1979, 1983; Bengtsson et al. 1980; Williams 1983; Dafni 1991; Köster 1991). See also Kearn & Inouye (1993) for an overview of odor collecting and analyzing techniques.

Dafni, Pollen. A primary component of the reproductive system but also serves in many cases as a reward for pollinators. In fact, next to nectar it is the
most common currency for payment of pollination services. Careful collection of pollen samples is an important step in many pollination studies and there are numerous other fields of research related to pollen. For determination of pollination syndromes it should be sufficient to differentiate between sticky or dry pollen, which can be done easily in the field.

Pollen can be collected successively in parts of the flower other than the anthers. This is important in understanding the transfer of pollen to the pollinator and the stigmaic surface and should be observed in the field. For further studies and identification of pollen species, pollen samples can be collected in closed anthers from flower buds and from pollinators.

The amount of pollen may change depending on the compatibility system of the species. Less pollen is released if flowers offer other rewards and pollinators do not feed on pollen. However, the direct costs of reproduction may have been underestimated and pollen, nectar, and resin production probably consume as much or more of tropical forest primary net production as folivores and frugivores do (Roubik 1993a). For studies on pollens/xenodochy, their ratio, and their relation to pollination and breeding systems, see Cruden (1977), Channou (1979), Queller (1984), Berlin (1986), and Lover Duarte & Lover Duarte (1988). Modern cell counters and particle counters allow rapid study of many more pollen samples in a shorter time. They should be used to increase knowledge of breeding systems in tropical trees, which is also of economic and conservation interest.

For more detailed research related to pollen and stigma biology see: Dafni (1992) and Kearns & Inouye (1993).

Stigma. Stigma receptivity is a crucial stage in the maturation of flowers. It can influence self-pollination, pollination success and relative importance of pollinators. Uniformly no common protocol can be used to test receptivity in a large number of species. There are several tests described (Dafni 1992) but none of these works in all cases. Most of them might be difficult to apply in typical campylos for several reasons. See also Thomsen & Barren (1983), Arnedo (1982), Bern (1982), Macies (1986), Hervey (1987), Moore (1987), Ohsborn et al. (1988), and Preston (1991).

Estimation of pollen load on the stigma can be used as an initial criterion for pollinator visitation/infertility and is easily obtained. It can be used in combination with techniques to control pollinating visiting on single flowers in order to obtain information on the efficiency of pollen transport by a given pollinator. Shaner & Geanakopoulus (1990) review the relationship between patterns of pollen deposition and numbers of seeds per fruit.


Nectar standing crop and nectar production (Pierson & Zimmermann 1983, Poutling 1989, Waser & Mitchell 1990, Sweeney 1991) can be measured and sampled in the field with regular micro-pipettes if nectar amount is more than 0.5 μl. For smaller amounts, special micro-pipettes and paper wedges can be used (Dafni 1992, Kearns & Inouye 1993). Sugar concentration can be measured in the field using refractometers (Costeb 1978, Baker & Baker 1982) which are available for different sugar concentrations (Dafni 1992, Kearns & Inouye 1993). If the amount of nectar is high enough, samples can be taken for further analysis of sugars and amino acids.

Other rewards. Oil and resin (Vidal 1963, 1974, 1986, 1990; Simpson & Neff 1983; Vidal & Mand 1991) can serve the same function as nectar. They should be investigated in order to understand the function and syndrome of pollination. Also, pheromones, floral tissues, bracts, stamens, and nectar, and nesting places (nesting sites) are rewards for pollinators offered by flowers (Simpson & Neff 1983).

Sexual stages of plants. Sexual systems of plants (Busa & Beach 1981) are related to gene flow, outcrossing rate, population structure, and genetic diversity. These attributes of plant populations are mediated and maintained by pollinator activity. The dependence of many plant species on animal pollinators
has enabled the evolution of mechanisms that effec-
tively reduce the probability of mating. As well as
dichogamy, the dechlorophyllation of male and female
strobili do occur in many species. For more details on dicho-
gamy in angiosperms, see Berber & Newman (1993)
and for detailed floral functional phenomena, see

To some extent the sexual system is easily re-
cognizable and therefore should be included in all
field protocols of pollination studies. The following
categories should be distinguished:
- bissexual and unisexual flowers
- moronemous, amennomomous, gynomonomous,
polygynomomous, dioecious, and indinomomous,
gynodioecious,
- unisexual plants,
- pantandric, protogynic, and herkogamous flowers;
- self-incompatible and self-compatable plants (based
on developed shots, includes simple experiments):
- heterostylous (distich, tristich) and unistraystlich
flowers.

Flowering phenology. Phenology refers to the seaso-
nal timing, succession, frequency, intensity, and sus-
tiation of flowers. [text continues] leaves. Flowering and
fruiting phenology should also be studied in relation to
leaf phenology because there may be strong intra-
plant and interspecific correlation between leaf fall or
leaf-shooting and flowering, especially in tropical
carrieties.

Phenology is related to individuals, populations,
communities, physical influences (temperature, day
length, altitude, latitude, water availability), biological
agents (predators and pollinators), to advertising and
reward system, and to season or allocation among
plants (e.g., cytoplasmic endosperm, gynoecium, and
bracteas) (Stevens 1993), flowering phenology is therefor
of significance for ecological and evolu-
tional reasons; it determines food resources for
pollinating animals and can be on isolation and
specialization on an evolutionary time scale. There are
diffrent leads to the study of phenology; the
single flower, single strobilus, the individual
plant (dioecious plants), the population, the com-
nunity, and phylogentic aspects. Newem et al.
(1994) provide a logical fowrness for quantitative
descriptions of complex phenological behavior
of tropical plants.

In me or cemal plants, bucles or cames may be
important when considered as sampling units
for phylogecical studies. Phylogecical data collected for
an entire community, or at least for 2 guilds, could
coonstall provide clear about factors that shape the
flowering curves. A variety of techniques has been
suggested for examining phenological data for
temporal bepreneces (Bode & Rathy 1979, Esta-
brook et al. 1962, Glawe 1982, Wace 1983,
Wagne & Paris de 1984, Murray et al. 1987,

Competition for pollinators (Berti 1976,
Campbell 1983, Keph & Wace 1985) may affect
pollination. Therefore neighboring plants with similar
flower types should be considered if phynology and
pollinization success of single species are being studied.

Pollination. For different techniques and methods
of vallcing, labeling, indentifying, and phying
insects and other pollinators, see Karmi & Jauque
(1993).

Pollinators should here be regarded as a
contiguous framework for studies. A typical hawk-
mesh flower may be visited by birds which may
contribute more to pollen transfer and seed produ-
tion than the expected hawk moth. The critical issue
is the pollination efficiency of a pollinator in terms of
the number of pollen grains transferred to the stigmate
surface, seed production, and the dif-
ferential contribution to the next generation.

Pollination behavior is important in relation to
pollination syndromes, distinction between pollina-
tors and other flower visitors, reward utilisation,
pollen disposal, careen use, pollination efficiency,
and energetics, etc. Patterns of movement
of pollinators are important because they will deter-
mine an important component of gene flow (Boskik et al. 1995). Two parameters have been used to quan-
tify flight patrol of flowers: first, flight distance
between two visited flowers and change in flight
introduced the qualitative terms "inner" and "major"
with reference to the foraging specializations of
bumblebees. Waddington (1983) reviewed studies in
this topic and presented reasons for using the more
general term "far-nestivation-Sequences." See also
Lewis (1986, 1986) and Wace (1986) for performance
and continuity in flowers visited by pollinators.

Pollen transfer can be studied by observing and
manipulating stigmas per flower (Newton & Rodnh,
& Thompson 1991). Density of flowering plants (and
flowers) can affect the foraging behavior and pro-

73
facilitability of foraging by pollinators, and hence their effects on pollination. Some studies have found correlations between flower density and visitation rates or seed set (Thomson 1981, Cribb & Zimmerman 1984, Schmitz et al. 1987, Allison 1990), but others have found none (Roubik & Allsopp 1982, Schmitz 1985). Visitations have been shown to increase with plant height (Hattiswurth et al. 1984, Lauer & Lason 1990) or to decrease with plant size (Anderson 1980). Visitations rates have also been shown to vary with inflorescence size (Willson & Benis 1979, Thomson 1988).

Nectar and pollen are the main caloric rewards in flowers. Heske & Raven (1972) pointed out the importance and the implications of pollination energetics in relation to the utilization of flowers as food sources. Optimal foraging theory assumes that animals have evolved through natural selection to forage efficiently (Pyke 1978a, b). Studies on pollina-
tion energetics may deal with various aspects of foraging behavior with regard to the energetic gain at various levels from the animal viewpoint as well as from the plant viewpoint, and their interaction. Dafni (1992) gives an overview of the main com-
ponents of foraging behavior and the energetic balance concerning pollination.

Roubik (1994a) gives field data on tropical forest stratum association of twenty bee species and dis-
cusses the theory of canopy preferences of large bees pollinating tropical flowers in the light of foraging behavior which might produce stratum and floral fluidity.

Geno-flow. Gene flow in natural plant populations is, determined by seed and pollen flow. Except in species where the seed dispersal mechanism is more spe-
cialized, e.g., mediated by water (Walker et al. 1982) or animals (Beattie 1978), the seed flow component of gene flow may be of minor importance relative to the pollen flow component (Levin & Kareiva 1968, Campbell & Water 1989). In the pollen flow com-
ponent of gene flow in insect-pollinated plants, the pollinator and their movement through the plant population has a profound influence on the bree-
digital structure as well as on the genetic structure of the population (Levin 1978, 1985; Schmitz 1983). The pollinators are, however, in their turn influen-
ced by the spatial structure of the plant population because of plant density and distribution affect the mo-
vements of pollinators and thereby the dispersal pat-
tern of pollen (Levin & Kareiva 1969a, b, Schaal 1978, Schmitz 1983; Roubik et al. 1995).

In animal-pollinated plants, gene flow distances are rather short (Levin 1988), but long distance polliination frequently occurs in the canopy and indicates of tropical rain forests. Several authors have hypothesized that the high diversity of tropical me spe-cies is a product of non-adaptive speciation resulting from introgression and genetic drift (Cor-
nor 1994, Baker 1995, Fuelev 1966, van Steenis 1969). In terms of sexual and breeding systems, however, there is much evidence that a majority of tree species in tropical canopies are outcrossed.

An alternative hypothesis, the microspecies equi-
librium hypothesis, originally proposed by Dobr-
sky (1950), contends that tropical me diversity results from the adaptation of me populations to very specific niches defined by body, biotic and abiotic components (pollinators, seed dispersers, soil, light, succession, seed predators, etc) (Stanley 1973, Con-
nall 1978, Hubbard 1979, Dettling 1987, Bawa 1990). This hypothesis requires low inbreeding and high effective population sizes. Genetic markers can be used to estimate the relative frequency of out-
crossing, selfing, and apomix in tropical me spe-
cies (O’Malley & Bawa 1987), and to estimate gene flow, effective population size and genetic variation in populations (Bawa & Konagai 1990).

Comprehensive data on flowering patterns, floral rewards, and sexual systems are required to under-
stand the structure and functioning of reproductive systems at the level of species and communities and the specificity of plant-pollinator interactions. Li-
miting factors for pollinator recruitment and the composition of pollinator guilds in the canopy and understory are of theoretical and practical interest, as they influence pollinator dispersed, gene flow, and ge-
diversity within the tropical forests (Doligez & Joly 1997a, b).

SEED DISPERSAL
Description of study site. Vegetation types, structure of the canopy, altitude, and climate, including light quality and quantity, should be described precisely because they strongly influence spatial and temporal distributions of fruit and frugivores.

Dispersal patterns. They are measured for indivi-
dual plants, seed dispersers, and recruiting. Six main types of structural distribution are distinguished: uniform, with density variation, by zones, packed, clumped, and with two scales of hetero-
gencity(e.g., Jaffé 1997). These distributions are

74
tuned using the spatial autocorrelation matrix method (Chowell 1981), or visual and local variability following Chowell 1981, chs by Julian 1955). Seed distribution patterns are generally expected to follow a negative exponential form (see Young 1995), and are tested by their slope, the modal distance and the maximum dispersal distance (e.g., Wilcock 1995), or by Morisita’s index of dispersion (e.g., Hoyle 1995). Relative spatial distribution patterns are also tested using the variance in mean trait (Wilson 1977) compared with expected values based on random distribution generated by Monte Carlo simulations (e.g., Lawell & Blake 1993), or the spatial Mantel test (e.g., Hoyle 1995). Mean nearest neighbor distances are also used to investigate spatial aggregation with respect to spatial scale with Clark and Evans’ index of aggregation (see Horvitz & Le Corff 1993).

functionary to define functional groups of fruits or dispersal syndromes. Fruit is considered for its functional importance in the dispersal process, not for its entogenetic meaning of enlarged may. However, prey care should be taken over functional homology of structural morphology for purposes of fruit classification (van der Pijl 1982). Seed dispersal syndromes retaining several of these fruit characters into consideration have been described by van der Pijl 1982, Janzen 1983, Gabri Hertl et al. 1985, Kubikl 1985, Howe & Westley 1986, Downum-Lemmon 1988, and Williams et al. 1990. These dispersal syndromes include endocarps (berry, capsular, drupe, or pod with ingested fleshy pulp or skin), chitinochorphy (green or yellow multiple fruit), endocarps (black or brightly coloured fruit with morphological differences relating to fragility specialization, suctomcho (lightly coloured fruit, fruit smeleng, growing near the ground or dropping at maturity), myrmecochory (with a charismate which is attractive to ants), malnchory (Wilcock & Young 1995), with fruit that produces avis as an attractant for bees, synchorphy (fruit rich inhaus, baits or sticky substances that cling to the fur of humans), anemochory (dry fruit with wings, plumes or hair that increase air resistance), and autochory (the disperse is ejected explicitly from a seed-pod). For cases of interspecific differences in fruit choice for consequences for fruit selection, see also review by Moorman & Dismuke 1983, 1985, and Fuentes 1994). For a review of plant traits that are thought to be casued or non-acclimated with fragilicious seed dispersal syndromes, see Fleming 1992, and McRitchie & Bemer 1994.

- Life and growth form of plant are described using common botanical categories. Life forms are important since they may relate to dispersal syndromes (e.g., Keay 1957, Hughes et al. 1994).
- Influences of fruit accessibility, ripeness, size, or spacing on fruit choice by tropical birds have been studied using experimental protocols and field observations, by Dark & Mouton (1982), Mouton & Demoule (1983, 1985), Lecoy et al. (1984), Demoule et al. (1988), Lecoy (1987d), and Lasne & Blake 1990. For behavioral studies of fruit choice in captivity, a synthetic diet simulating colored berries can be used to maintain and study fruit-eating birds (Demoule et al. 1987).
- Fruit size and seed size contribute to dispersal syndromes and influence feeding behavior and seed dispersal. Fruit size as a function of size of tropical fruits has been studied by Fitch & Stiles 1983, Westphal 1985, 1995, Lecoy 1987a, and Downum-Lemmon 1988. Westphal 1993 designed a protocol for understanding the evolution of fruit size and the potential for evolutionary response to selection by dispersers, which could be applied to other fruit taxa. Mazar & Westphal 1993 used a survey to explore the hypothesis that much variation in fruit size might be explained as the evolutionary outcome of selection by one-sensitive avian dispersers.
- Fruit and seed morphology is measured in three ways: puncturing resistance using instruments described by Kinyior & Nesom 1990, crushing resistance (e.g., Kirrnan & Norden 1993), and typing of external fruit resistance described by Sabate (cited in Julliot & Schuster 1933) the first two methods are the most reliable and should be chosen according to feeding behavior of studied frugivores.
- Chemical composition of fruit measures frugivores’ reward, in terms of dry weight of proteins, lipids and carbohydrate (e.g., Foster & McDaid 1983, Howe & Westley 1988). Few studies analyze the importance of secondary compounds in fruit pulp but see Barne et al. 1993 for sapstios, flavonoids and cyanogenic glycosides, Kersten & Potter 1994 for sapstios, and Tomatoes and tomatoes, and Burton et al. 1993 and Barra & Whiton 1994 for protein and fiber content; total phenols, condensed tannins, and alkaloids. "Standard for taxonomy analysis are recommended by Hageman & Baker (1989). Sugar testing ability has been studied experimentally in forest birds by Lecoy (1987c), and in
Studies of adaptive significance and consequences of flowering physiology for primary consumers. They have been conducted by van der Meijden et al. (1990). Samples of flowering trees on Corsica, and on primroses on Crete (1994). Worthington (1992) probably used the most detailed protocol to measure the effect of food supply on breeding rhythms and population size of flowering trees on an island. It requires a precise definition of diet, availability of food resources in energetic terms, and energetic demand for breeding activity of the whole bird population.

Pollinators for the assessment of fruit abundance and flowering time. They have been reviewed by Blake et al. (1996); and evaluated by Stubbins and Dinsen et al. (1980) for bees, and by Chapman and Waser (1994). Phenology of insects, or quadrats, each ideally including only one habitat type. are used to assess number and size of fruit crops by visual estimation using a relative rank, extrapolation from fruit counts of canopy subsets (see Chapman et al. 1992), or derivation from DBH or crown volume. Excessive monitoring of flowering trees is possible only when flowering plants have small ranges. Phenological studies and relative estimation of fruit abundance by fruit fall along trail systems are usually not useful in the estimation of fruit density. Chang & Wang (1995) compared relative advantages and disadvantages of fruit-trap collection, platform observation, and tracked-immature survey. Any of the three methods can be used for the approximation of annual flowering phenology, but that of fruit-trap collection is more accurate to measure the annual fruit production, and that of platform observation offers the best estimation of the quantity of fruit in the tree crown at a given time. Fruit-trap methods are time-consuming and cause several biases: nonrandom placement in heterogeneous environments, underestimation of fruit scarcity, collection of dropped, less preferred, or damaged fruits, underestimate of small-petioled, or small-seeded species, small size of sampling surface. Terborgh (1983) also discussed biases inherent to fruit-traps.

Recording visitor activity. Observational methods for behavior sampling have been reviewed by Altmann (1974) and Martin & Bateson (1993). Protocols include ad libitum sampling, sociometric matrix complex, focal-animal sampling, sampling all.
examination of various behaviors, sequence sampling, one-zero sampling, and instantaneous and scan sampling. Choice of a sampling technique depends on information required and observational conditions, although focal-animal, instantaneous, scan, or combinations of these methods appear better adapted to seed dispersal study. Optimization of data collection may be achieved with unprocessed data recording and analysis, such as The Observer system (Vinner 1993, Wassena 1994). For a review of behavioral data collection methods and equipment, see Lehrer (1990).

Fruition species, and when possible age and sex, have to be noted. Particular care has to be taken to evaluate relative accounts of both diurnal and nocturnal fruit consumption, and to sample frugivorous activity independently of time. Observation of frugivorous behavior at flowering times is evidently crucial for separating efficient seed-dispersers from seed-predators. Interspecific dominance hierarchy should be considered when monitoring large heterospecific feeding assemblages (e.g., Dudley & Eiblich 1994). When using bioecologic models, it is important to record time budgets according to feeding activity, such as measuring flight movements or perching time, possibly using radio-telemetry. Analyzing specific adaptation or coevolution between frugivores and fruiting plants requires measuring the availability of fruit to frugivores and analyzing feeding behaviors. Specific identification of dispersers is important to separate marasch, dropping many seeds under the parent tree, from gapers, ingesting fruit whole (Levy 1987a). Categories of fruit-handling behavior have been described by Levy (1986) and Foster (1987).

Dispersing fruit-food diets and diets. Different methods are used to define diet: direct visual recording (e.g., Haila 1977), which provides detailed information but is practicable only when conditions of visibility are excellent; stomach contents, and time spent feeding (Chambers-Brock 1977), which accurately describes feeding behavior but cannot be accepted as an estimate of food intake since feeding rate may differ considerably between food items. Comparison of these three methods to determine monkeys’ diets has been conducted by Haila (1977). The frequency method overestimates occasional or short consumption, but is considered as giving similar results in time budget measurements in particular species (Slovákova 1975, Chambers-Brock 1977). Direct observation, stabilization of fences (e.g., Levy 1986, Julian & Sabater 1993) and examination of regeneration contents, are often combined to define diets (e.g., Worthington 1982, Thomas 1988). Advantages and disadvantages of using focal samples to determine diets of birds has been discussed by Whelan et al. (1984) and Linell & Bååe (1990). In birds, diet can also be determined by food flotation or by forced regurgitation, methods whose efficiency have been compared by Poulton et al. (1994). Analysis of stomach contents is still practiced on homed animals (Gailloître et al. 1994). All indirect methods of diet definition require the use of a reference collection of fruits and seeds.

Evaluating the effectiveness of seed dispersal. Numerous studies analyze the contribution of dispersers to plant fitness, which depends on the quantity and quality of seed dispersal. A synthesis of current approaches to effectiveness of seed dispersal can be found in two books edited by Estrada & Herms (1986), and Herms & Estrada (1993). Effective seed dispersal requires seeds to escape from their parent tree (Jansen 1976; Cornell 1977), and to colonize a site: appropriate for germination and further development of seedlings (House & Smallwood 1982). Kupch (1993) reviews the available information and provides a framework for addressing disperser effectiveness. This approach is crucial for designing comparable studies.

• Differentiating legitimate dispersers from seed predators, either in trees or on the ground. This requires estimating the relative consumption of ripe and unripe fruit, and evaluating dispersal and traits during exploitation of fruiting palms (e.g., House 1986, Jardine 1983, Beck & Wong 1985, Sun et al. 1997). Behavioral differences should be carefully extrapolated, because seed treatment may relate to geographic variability of key plant resources (Gómez-Fojo et al. 1993).

• Estimating the eventual positive impact of seed consumers and secondary dispersal (specific marking of fruits and seeds which will be scattered-bored and partly forgotten by these secondary dispersers). For experimental manipulation of ant and rodent communities to evaluate their relative impact on vegetation, see Brown & Munger (1985) and Draculik et al. (1985). For relative roles of monkeys, rodents, and dung beetles, see Estrada & Guarisco-Estrada (1991). For protocols on myrmecochory, see Harver & Basir (1983), Hughes & Wensley (1990, 1992), Kaufmann et al. (1991), Byrne & Levy

77
(1993), Kaspary (1993), Levey (1993), Levey & Byrne (1993), and Horvitz & Schmecke (1994). Secondary seed dispersal has also been demonstrated in earworms (Willms & Hoja- jman 1994), fish (Goslee 1979, Gislaing 1980, Kullberg & Zbikowski 1994, Souza-Steva et al. 1994), reptiles (Rick & Bowma n 1961, Davon 1962, Carpes Figueira et al. 1994), and large ground rodents (e.g., Rodrigo et al. 1993, Fox 1995). Differenti- ating seed predation by vertebrates and invertebrates is usually done with seed exudates (e.g., Forbush et al. 1993). Transport of seeds by food-harvesting animals has been studied with radiocarbo-needed seeds, radio-tagged and metal-tagged seeds (Price & Jenkins 1986), coded thread passed through seeds (e.g., Forber 1993), or recovery of marked large seeds (e.g., Mack 1995). Van der Wall (1990) reviewed studies of seed dispersal in fruit-feeding animals, and Price & Jenkins (1986) methods to measure seed harvest, secondary transport, and caching by rodents.

- Estimating the possible negative impact of dispersal of seed-plyoric insects by frugivores. For studies investigating insect survival after passage of ingested seeds through bird guts and their dissemi- nation by birds, see Nakajima & Prince (1994) and Gute & Rain (1995).

- Measuring digestive transit time and assimila- tion efficiency as adaptation to frugivory has been studied by Wodrich (1989) and Boc and Parra (1992) on tropical birds. Paper layers (Levey 1986), or colored and radio-opaque markers are used to monitor intestinal transit (e.g., Herrera 1986, Milton 1996, Jedore 1997). Kanan & Levey (1990) used 843 labeled fruits for measurement of transit time, in vivo measurement of intestinal uptake of nutrients, and double-isotope method to measure digestive efficiency.

- Activity and movements of dispersers should be monitored as precisely as possible, ideally by using radio-tracking (e.g., Cooper & Charles-Dominique 1985, Flemming 1988, Charles-Dominique 1991). Relative location of fruiting sites, mating sites, shelters, and sleeping sites should be taken into account since they may constrain seed dispersal (e.g., Thury & Legris 1993, Julitte 1997, Krüger et al. 1997).

- Quality of seed dispersal has been studied by observation and experiment (e.g., Hsiao 1977, 1993 and previous papers on dispersal of Vitis vinifera), and for a modeling approach (e.g., Horvitz & Schmecke 1986, Murray 1988, 1988, Maritines- Ramos & Alvarez-Buylla 1995). Other methods include comparing seed rain, seedling, and tree communities (e.g., Maritines-Ramos & Sam-Castro 1993, Julitte 1997), evaluating mean dispersal distance by direct observation (e.g., Julitte 1996), comparison of transit time and distance traveled (Sant et al. 1997). However, Schupp & Fuentes (1995) showed that a correspondence, or a lack of correspondence, between patterns of seed arrival and adult recruitment tells us little about causal rela- tionships and dispersal quality. They suggest com- bining observation and experiments, taking into account complexities of recruitment, and manipu- lating patterns of seed arrival and causal modeling.

- Comparing germination rates of seeds ingested or not by dispersers. Germination tests are conducted on seeds taken from feces and uncomposted seeds taken from fruits collected in situ under trees visited by frugivores. Two criteria are usually used to account for determining the effect of frugivory on seed germination: germination rate and speed (Hladik & Hladik 1963, Estrada & Contreras-Estrada 1984, Hladik 1986). Similar studies have been conducted on seeds whose aril has been removed by ants (Horvitz & Brasier 1988).


Decomposition of fruits, seeds, and fragrants. This should be managed through standardized data banks including color photographs.

PRACTICAL SUGGESTIONS FOR DATABASE IMPLEMENTATION

General considerations. The topic "pollination" and "seed dispersal" can be looked upon as part of what is called "plant-animal interaction" (I.M.). We will use this broader term in this context and in the entity- relationship diagram given in Fig. 2. Databases designed for PM data should be implemented so that they can be used for storing both complete and partial data and, as a working database, for storing incomplete and "raw" field data. This point has con- siderable influence on the database structure needed, because, in the latter case, almost all data including the names of the taxa involved could be lacking. The
FIG. 2. Entity-relationship diagram for plant-animal interactions.
“worst” case would be that the only data present at a time of first data entry is “a certain person observed a certain interaction at a certain time.” It must be possible to enter all additional data later on.

Database design. The basis for all data on interaction is, therefore, an observation of one or more persons at a certain location at a certain time (Fig. 2). The source of information can be a direct observation or cited from literature.

The organisms (involved group of organisms) can be one or more plant(s) and/or animal(s) which are characterized by their scientific name (plant and animal), their common name (vernacular name), and/or by vouchers (collection). This technique allows for entering or changing the denominations of the taxa at any time. The collections need not only be vouchers for a specific observation but can also be samples of any kind for further chemical or histo- logical investigation.

The way of storing the synonyms and the determinations shown in Fig. 2 allows for later queries according to the nomenclature valid at that time. To achieve this, only the synonyms has to be changed once and now the determination of all voucher specimens separately.

The data on an observation are text (text), which is the simplest case in tabular terms, or other multimedia objects (image/video/audio). Besides being stored as a plain text the observation data can also be broken down to single characters and their states. In the latter case a distinction has to be made between those data which are specific for the observed interaction (specific information on animal / plant) and those which are not (characters and states). For example, the observation of the character “number of stamens” can either be a useful character for a plant, and thus be unrelated to the observed interaction, or considered as dependent on or important for the observed interactions, and must then be stored in relation to the interaction itself. Another example might be flower colour changing during the lifetime of the flower. In short, this distinction is important in all those cases where a character might vary, but the state of this character at a certain time and a certain locality is of importance.

Each dataset entered (interaction) is also described by one or more key words out of a hierarchically listed (kind of interaction). The key words categorize the entered data with the appropriate terms, e.g., polymorphism, endosmoshy, fragility, and so on and describe, for example, the parts of the animal (e.g., tentacle, antennae) and plant (e.g., leaf, flower, stems) involved in the interaction. By this procedure the data from different personal observations and from different publications can be made comparable and accessible for retrieval.

The entry general information refers to all abiotic factors as a certain locality like wind speed, wind direction, temperature, and humidity.

Existing standards. Existing biological and ecological standards and protocols should be used. There are different standards for database structure, data charac- terization, and data exchange formats. Where possible the standards developed by the International Working Group on Taxonomic Databases for Plant Sciences (TDWG) should be used for the botanical context (Bedny 1995). Modelling of collection data can be done accor- ding to the ASC (ASC 1993) and/or the CDFEd (Bednárova et al. 1996) standards. Although there are these two, and even more, competing models it should be pointed out that implementations based on the same standard might vary considerably in detail. Important details on collection data can also be found in the HISFED (Cnife 1992) and POSS standard (Giller et al. 1995).

Characterization of plant parts can be done ac- cording to the TDWG Standard of Economic Bo- tany Data Collection Standard (Cook 1995, for an implementation see Book & Hoppé 1996). It con- tains a master list of plant parts which must be com- plemented by adding missing plant parts if necessary. The World Geographic Scheme for Recording Plant Dis- tributions (Hoffman & Brummitt 1992) can be used for geographic descriptions. TDWG standards for plant life forms and vegetation types are in preparation.

Complex exchange of data between different da- tabase systems can be carried out with the XDF for- mat (Afflin & White 1988). A simple data exchan- ge can be done via file transfer whereas possible, par- ticular for the transfer of data from a older pro- gram or when exporting data to statistical programs. Further standards exist for plant names (Brummitt & Powell 1992) and herbarium acronyms (Holmgren et al. 1990).

New standard. A hierarchical system of key words for the characterization of interaction data (slend of interaction) must be developed. Based on the various sources mentioned above, a master list of key words should first be developed for pollination and sex
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