ANGIOSPERM POLLINATION AND SEED DISPERSAL, A REVIEW

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Abstract. This review aims to provide a common conceptual and methodological framework to studies of Angiosperm pollination and seed dispersal conducted in tropical forest canopy. We review, briefly describe, and eventually compare protocols designed to measure environmental and microclimatic parameters, life and growth form, morphology and other attractive or protective characters (color, odor, texture, chemical composition), spatial and temporal distribution patterns, resource abundance, visitor activity and diet, and the effectiveness of pollen and seed dispersal. Particular emphasis is given to methods adapted to tropical forest canopy research, usually transferred or modified from ground-level techniques. Plant and animal characteristics involved in mutualistic or coevolutionary processes are considered in bioenergetical terms related to investment, reward, and resource allocation dedicated to Angiosperm and frugivore reproduction. Practical suggestions for common database implementation are made, together with a presentation of existing and new standards. *Accepted 21 July 1998.*

Key words: Angiosperm, pollination, seed dispersal, tropical forest, canopy, methodology.

INTRODUCTION

The aim of this review is to provide a common framework of data collection in order to promote standardization of comparative studies. For the understanding of Angiosperm reproduction, bioenergetic concepts related to investment, reward, and resource allocation must be considered. Although tropical forest canopy poses conditions for pollination and seed dispersal that are distinct from understory levels, common techniques used in studies of tropical pollination and seed dispersal at ground level can, in general, be applied to high canopy research. However, there are certain differences when studying pollination and seed dispersal in tropical canopies, most of them related to the structure of the canopy and the accessibility of tropical canopies.

This report does not try to give a complete overview of protocols used by pollination ecologists and seed dispersal biologists. The short descriptions of methods and detailed bibliographic references on specific techniques focus on tropical forest research. Only some important points, and which to us seem to be of major importance, are here discussed.

POLLINATION

Besides single rope climbing techniques (Perry 1978, Perry & Williams 1981, Mitchell 1982, Dieterlen & Nill 1993) a set of different canopy access methods like masts and cranes, canopy walkways (Inoue *et al.* 1995, compare Dieterlen & Nill 1993), balloons (Hallé & Gaillarde 1990, Hallé & Pascal 1992, Hallé 1998), and gondola systems (Gottsberger & Döring 1995) have been developed to enhance canopy access.

For more complete information on common protocols in pollination ecology there are Dafni's practical approach in *Pollination Ecology* and Kearns & Inouye's *Techniques for Pollination Biologists*. For references on reproductive biology and genetics of trees in tropical canopies, see Murawski (1995), and for progress in pollination ecology in recent years see Gottsberger (1985, 1989, 1993, 1996).

Each part of flowers or blossoms (*sensu* Faegri & van der Pijl 1979) can have a special role in pollination and during 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 (scent, 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 mature tropical forest trees and epiphytes, because non-pioneer forest trees commonly do not resprout asexually 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).

Description of study site. Temporal and spatial heterogeneity of canopy structure has a strong influence on pollination ecology. By altering climatic factors and offering resources, tree crowns influence the foraging of pollinators (Roubik *et al.* 1995) and seed dispersal agents. Because of the high heterogeneity of tree crowns, special effort should be applied to charac-
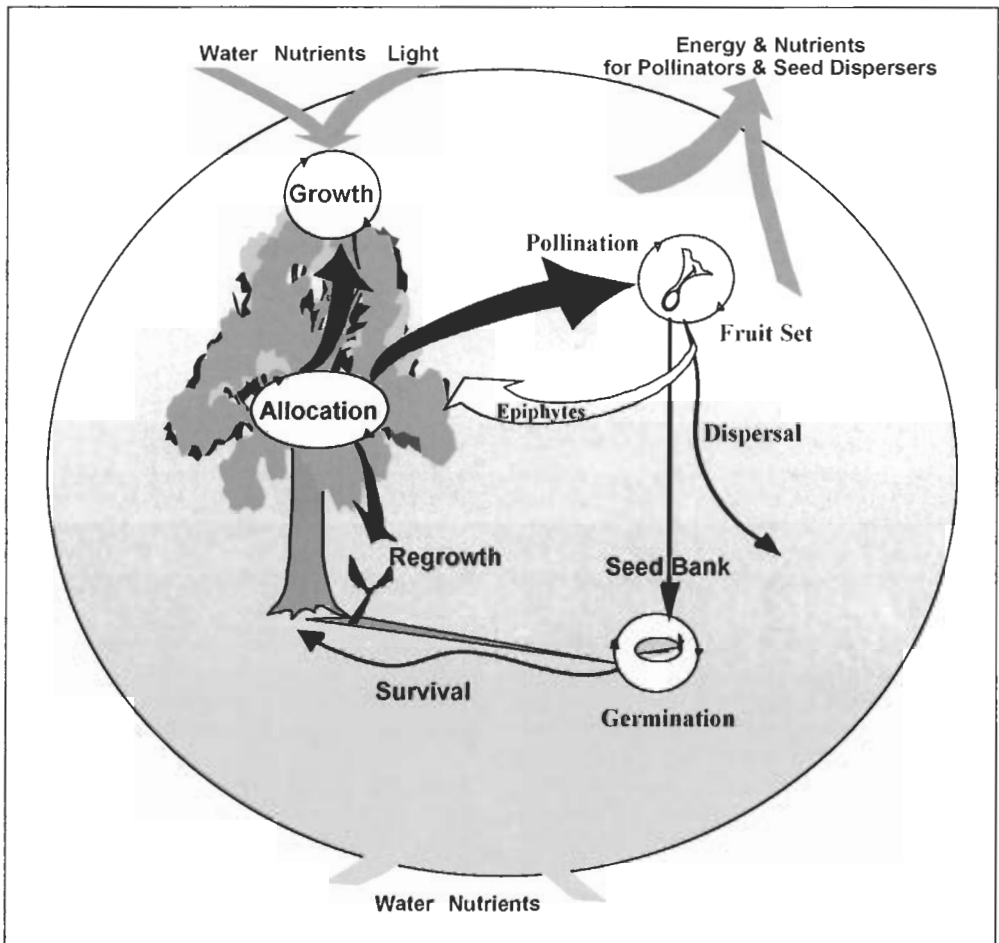

FIG. 1. Important steps in canopy plant life cycles. Key factors of the ecology of tropical forest canopies are the allocation of resources to flowers, fruits, and seeds versus vegetative growth and the interaction with animal vectors in pollination and seed dispersal.

terizing structural, micro-climatic, and phenological aspects in all studies of pollination ecology in tropical canopies (see Hallé 1995, Parker 1995).

Disrribution patterns of flowers and plants, nearest potential reproductive partner, density, frequency of flowers and plants related to height or layer of canopy, and growth forms of plants may be of special interest in canopy pollination ecology.

Position and orientation of flower. The spatial position of flowers and the structure and organization of inflorescences are regarded as adaptations for effective pollination. Flower position can be studied relative ro plant axis and/or to horizontal and vertical axes. In canopy studies it is of importance to note the position of single flowers or inflorescences (e.g., of epiphytes) relative to tree crowns and leaf layers because of their visibility and accessibility to pollinators. Microclimatic heterogeneity and light environment (Clark *et al.* 1989, Endler 1993, Freiberg 1997) should be considered in more detail regarding their strong influence on pollinator behavior.

Inflorescence structure. The structure of an inflorescence is likely to influence factors such as the foraging efficiency of flower visitors, the degree of outcrossing, and other aspects of plant reproductive success. Schemske (1980) found that reproductive success in a pollinator-limited orchid varied significantly with inflorescence size, and Wyatt (1982) reviewed data on how inflorescence architecture affects pollination and fruit set. Weberling (1989) presents a complex vocabulary to describe inflorescence morphology.

Flower morphology. Floral morphology is of both taxonomic and ecological interest. It can genetically isolate different species through polystyly, or reduce selfing through herkogamy, by placing pollen on distinct parts of a common pollinator's body. Flower morphology should be studied in order to understand its functional aspects. But floral measurements should also be taken in order to study intraspecific variation, which may influence components of male and female fitness (Beare & Perkins 1982, Stanton *et al.* 1991). Interspecific differences can provide insight into differences in pollinator guilds and resource partitioning.

A list of floral functional morphology in relation to pollination is given by Dafni (1992), who also presents a short list of the main blossom types and their functional characteristics (see also Faegri & van der Pijl 1979).

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 studied as part of a broader advertisement context. Flower color has been analyzed with respect to community spectra, seasonal aspects, specific pollinators, flower lifetime changes, and intraspecific variability. Flower colors attract and guide pollinators (Waser & Price 1981, Kevan 1983) and signal pollen or nectar availability or location (Gori 1983, 1989; Weiss 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 ultraviolet reflectance patterns, see Willmer & Corbet (1981, 1989), Joel *et al.* (1985), Macior (1986), Inouye & Pyke (1988), Menzel (1990), and Menzel & Backhaus (1991).

Flower odor. Fragrances may be as important as colour in advertising for pollinators. Special scent glands (osmophores) have been discovered (Vogel 1990) but most flowers show a diffuse production of scents and produce several different compounds. For a review of the trends in scent chemistry in pollination syndromes, see Knudsen & Tollsten (1993), and Dobson (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), most of them for experimental situations and not applicable in canopy research. For localization of osmophores, see Vogel (1963, 1990). For rapid description 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 odors. Recently, small devices for scent collection in the field have been developed, which allow analysis of the chemical compounds by gas chromatography and mass spectrometry (Nilsson 1979, 1983; Bergström *et al.* 1980; Williams 1983; Dobson 1991; Kaiser 1991). See also Kearns & Inouye (1993) for an overview of odor collecting and analyzing techniques.

Pollen. Pollen is 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 collecting of pollen samples is an important aspect of 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 dusty pollen, which can be done easily in the field.

Pollen can be presented secondarily in parts of the flower other than the anthers. This is important in understanding the transfer of pollen to the pollinator and the stigmatic 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 needed 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 of tropical forest primary net production as folivores and frugivores do (Roubik 1993b). For studies on pollen/ovule ratio, and their relation to pollination and breeding systems, see Cruden (1977), Charnov (1979), Queller (1984), Bertin (1988), and Lovett Doust & Lovett Doust (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 our 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. Unfortunately no common protocol can be used to test receptivity in a larger number of species. There are several tests described (Dafni 1992) but none of them works in all cases. Most of them might be difficult to apply in tropical canopies for several reasons. See also Thomson & Barrett (1981), Arnold (1982), Bertin (1982), Macior (1986), Herrera (1987), Morse (1987), Osborn *et al.* (1988), and Preston (1991).

Estimation of pollen load on the stigma can be used as one criterion for pollinator visits/intensity and is easily obtained. It can be used in combination with techniques to control pollinator visits on single flo-

wers in order to obtain information on the efficiency of pollen transport by a given pollinator. Shaanker & Ganeshaiah (1990) review the relationship between patterns of pollen deposition and numbers of seeds per fruit.

Nectar. Nectar is produced from phloem sap by active secretion in floral and non-floral glands. Floral nectar is a sugary solution with major calorific components like sucrose, fructose, and glucose (e.g., Barnes *et al.* 1995). Chemical composition of nectar is known to relate to pollinator type and visitation (Waller 1972, Hainsworth & Wolf 1976, Stiles 1976, Baker & Baker 1983, Bertsch 1983, Martinez del Rio 1990, Dafni & Kevan 1993, Galetto *et al.* 1993, Galetto 1995). Nectar also contains variable amounts of different amino acids and various minor components like lipids, pigments, proteins, alkaloids, electrolytes, and antioxidants (Pyke & Waser 1981, Baker & Baker 1982, Hiebert & Calder 1983, Gottsberger *et al.* 1989, 1990, Phamdelegue *et al.* 1994).

Nectar standing crop and nectar production (Pleasants & Zimmerman 1983, Possingham 1989, Waser & Mitchell 1990, Stevens 1991) can be measured and sampled in the field with regular micro-pipettes if nectar amount is more than $0.5\,\mu l$. 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 (Corbet 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 resins (Vogel 1963, 1974, 1986, 1990; Simpson & Neff 1983; Vogel & Machado 1991) can serve the same function as nectar. They should be investigated in order to understand the function and syndrome of pollination. Also perfumes, floral tissues, brood sites, shelter and heating, and meeting places (mating sites) are rewards for pollinators offered by flowers (Simpson & Neff 1983).

Sexual systems of plants. Sexual systems of plants (Bawa & Beach 1981) are related to gene flow, outcrossing rates, 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 effectively reduce the probability of selfing. As well as dichogamy, the desynchronization of male and female phases in a single flower, self-incompatibility systems, and polymorphisms like male and female sterility do occur in many species. For more details on dichogamy in angiosperms, see Bertin & Newman (1993) and for selfing and related functional phenomena, see Jarne & Charlesworth (1993).

To some extent the sexual system is easily recognizable and therefore should be included in all field protocols of pollination studies. The following categories should be distinguished:

– hermaphroditic and unisexual flowers;
– monoecious, andromonoecious, gynomonoecious, polygamomonoecious, dioecious, androdioecious, gynodioecious, trioecious plants;
– protandric, protogynic, and herkogamic flowers;
– self-incompatible and self-compatible plants (based on developed seeds, includes simple experiments);
– heterostylic (distilic, tristilic) and enantiostylic flowers.

Flowering phenology. Phenology refers to the seasonal timing, sequence, frequency, intensity, and duration of flowers, fruits, and leaves. Flowering and fruiting phenology should also be studied in relation to leaf phenology because there may be strong intraplant and interspecific correlation between leaf fall or leaf shooting and flowering, especially in tropical canopies.

Phenology is related to individuals, populations, communities, physical parameters (temperature, day length, altitude, latitude, water availability), biological agents (predators and pollinators), to advertisement and reward structure, and to resource allocation within plants (e.g., epiphytes like orchids, gesneriads, and bromeliads) (Stevens 1991). Flowering phenology is therefore of significance for ecological and evolutionary reasons; it determines food resources for pollinating animals and can act on isolation and speciation on an evolutionary time scale. There are six different levels to the study of phenology: the single flower, single inflorescences, the individual plant (dioecious plants), the population, the community, and phylogenetic aspects. Newstrom *et al.* (1994) provide a logical framework for quantitative description of complex phenological behavior of tropical plants.

In trees or clonal plants, branches or ramets may be important when considered as sampling units for phenological studies. Phenological data collected for an entire community, or at least for a guild, could potentially provide clues about factors that shape the flowering curves. A variety of techniques has been suggested for examining phenological data for temporal heterogeneity (Poole & Rathke 1979, Estabrook *et al.* 1982, Gleeson 1982, Waser 1983, Fleming & Partridge 1984, Murray *et al.* 1987, Rathke 1988, Pleasants 1990).

Competition for pollinators (Beattie 1976, Campbell 1985, Kohn & Waser 1985) may affect pollination. Therefore neighboring plants with similar flower types should be considered if phenology and pollination success of single species are being studied.

Pollinators. For different techniques and methods of collecting, labeling, identifying, and preserving insects and other pollinators, see Kearns & Inouye (1993).

Pollination syndromes have to be regarded as a conceptual framework for studies. A typical hawk-moth flower may be visited by bees which may contribute more to pollen transfer and seed production than the expected hawk-moth. The critical point is the pollination efficiency of a pollinator in terms of the number of pollen grains transferred to the stigmatic surface, seed production, and the differential contribution to the next generation.

Pollination behavior is important in relation to pollination syndromes, distinction between pollinators and other flower visitors, reward utilization, pollen dispersal, carryover and use, pollination efficiency and energetics, etc. Patterns of movement of pollinators are important because they will determine an important component of gene flow (Roubik *et al.* 1995). Two parameters have been used to quantify flight patterns of flower visitors: flight distance between two visited flowers and change in flight direction (Waddington 1979). Heinrich (1976, 1981) introduced the qualitative terms "minor" and "major" with reference to the foraging specializations of bumblebees. Waddington (1983) reviewed studies on this topic and presented reasons for using the more general term "floral-visitation-sequences." See also Lewis (1986, 1989) and Waser (1986) for preferences and constancy in flowers visited by pollinators.

Pollen removal can be studied by observing and manipulating visits per flower (Snow & Roubik 1987, Schmid-Hempel & Speiser 1988, Wilson & Thomson 1991). Density of flowering plants (and of flowers) can affect the foraging behavior and pro-

fitability 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, Cibula & Zimmerman 1984, Schmitt *et al.* 1987, Allison 1990), but others have found none (Roubik *et al.* 1982, Schmitt 1983). Visitation has been shown to increase with plant height (Hainsworth *et al.* 1984, Larson & Larson 1990) or to decrease with plant size (Andersson 1988). Visitation rates have also been shown to vary with inflorescence size (Willson & Bertin 1979, Thomson 1988).

Nectar and pollen are the main calorific rewards in flowers. Heinrich & Raven (1972) pointed out the importance and the implications of pollination energetics in relation to the utilization of flowers as food resources. Optimal foraging theory assumes that animals have evolved through natural selection to forage efficiently (Pyke 1978a, b). Studies on pollination energetics may deal with various aspects of forager 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 components of foraging behavior and the energetic balance concerning pollination.

Roubik (1993a) gives field data on tropical forest stratum association of twenty bee species and discusses the theory of canopy preferences of large bees pollinating tropical flowers in the light of foraging behavior which might produce stratum and floral fidelity.

Gene flow. Gene flow in natural plant populations is determined by seed and pollen flow. Except in species where the seed dispersal mechanism is more specialized, e.g., mediated by water (Waser *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 & Kerster 1968, Campbell & Waser 1989). In the pollen flow component of gene flow in insect-pollinated plants, the pollinators and their movement through the plant population have a profound influence on the breeding structure as well as on the generic structure of the population (Levin 1978, 1983; Schmitt 1983). The pollinators are, however, in their turn influenced by the spatial structure of the plant population because plant density and distribution affect the movements of pollinators and thereby the dispersal pattern of pollen (Levin & Kerster 1969a, b; Schaal 1978; Schmitt 1983; Roubik *et al.* 1995).

In animal-pollinated plants, gene flow distances are often short (Levin 1988), but long distance pollination frequently occurs in the canopy and understory of tropical rain forests. Several authors have hypothesized that the high diversity of tropical tree species is a product of non-adaptive speciation resulting from inbreeding and genetic drift (Corner 1954, Baker 1959, Federov 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 microniches equilibrium hypothesis, originally proposed by Dobzhansky (1950), contends that tropical tree diversity results from the adaptation of tree populations to very specific niches defined by both biotic and abiotic components (pollinators, seed dispersers, soil, light, succession, seed predators, etc.) (Janzen 1970, Connell 1978, Hubbell 1979, Denslow 1987, Bawa 1990). This hypothesis requires low inbreeding and high effective population sizes. Genetic markers can be used to estimate the relative frequency of outcrossing, selfing, and apomixis in tropical tree species (O'Malley & Bawa 1987), and to estimate gene flow, effective population size and genetic variation in populations (Bawa & Krugman 1990).

Comprehensive data on flowering patterns, floral rewards, and sexual systems are required to understand the structure and functioning of reproductive systems at the level of species and communities and the specificity of plant-pollinator interactions. Limiting factors for pollinator recruitment and the composition of pollinator guilds in the canopy and understory are of theoretical and practical interest, as they influence pollen dispersal, gene flow, and genetic 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.

Distribution patterns. They are measured for individual plants, seed shadows, and recruitment. Six main types of structured distribution are distinguished: uniform, uniform with density variation, by zones, packed, clumped, and with two scales of heterogeneity (e.g., Julliot 1997). These distributions are

tested using the spatial autocorrelation matrix method (Chessel 1981), or overall and local variability following Chessel (1978, cited by Julliot 1997). Seed distribution patterns are generally expected to follow a negative exponential form (see Houle 1995), and are tested by their slope, the modal distance and the maximum dispersal distance (e.g., Willson 1993), or by Morisita's index of dispersion (e.g., Houle 1995). Relative spatial distribution patterns are also tested using the variance to mean ratio (Pielou 1977) compared with expected values based on random distribution generated by Monte Carlo simulations (e.g., Loiselle & Blake 1993), or the partial Mantel test (e.g., Houle 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).

Inventory to define functional groups of fruits or dispersal syndromes. Fruit is considered for its functional importance in the dispersal process, not for its ontogenic meaning of enlarged ovary. However, great care should be taken over functional homology of structural morphology for purposes of fruit classification (van der Pijl 1982). Seed dispersal syndromes taking several of these fruit characters into consideration have been described by van der Pijl (1982), Janson (1983), Gautier-Hion et al. (1985), Kubitzki (1985), Howe & Westley (1986), Dowsett-Lemaire (1988), and Willson et al. (1990). These dispersal syndromes include endozoochory (berry, capsule, drupe, or pod with ingested fleshy pulp or aril), chiropterochory (green or yellow multiple fruit), ornithochory (black or brightly coloured fruit with morphological differences relating to frugivore specialization), saurochory (brightly coloured fruit, foul smelling, growing near the ground or dropping at maturity), myrmecochory (with an elaiosome which is attractive to ants), mellichory (Wallace & Trueman 1995, with fruit that produce resin as an attractant for bees), synzoochory (fruit with hooks, barbs or sticky substances that cling to fur or feather), anemochory (dry fruits with wings, plumes or hairs that increase air resistance), and autochory (the diaspore is ejected explosively from a seed-pod). For causes of interspecific differences in fruit choice and consequences for fruit selection, see also reviews by Moermond & Denslow (1983, 1985), and Fuentes (1994). For a review of plant traits that are thought to be coevolved or non-coevolved with frugivorous seed-dispersing vertebrates, see Fleming (1991), and Ricklefs & Renner (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 observation, by Denslow & Moermond (1982), Moermond & Denslow (1983, 1985), Levey et al. (1984), Denslow et al. (1986), Levey (1987a), and Loiselle & 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 (Denslow et al. 1987).

• Fruit size and seed size contribute to dispersal syndromes and influence feeding behavior and seed dispersal. Fruit choice as a function of size of tropical fruits has been studied by Pratt & Stiles (1985), Wheelwright (1985, 1993), Levey (1987a), and Dowsett-Lemaire (1988). Wheelwright (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 traits. Mazer & Wheelwright (1993) used allometry to explore the hypothesis that much variation in fruit form might be explained as the evolutionary outcome of selection by size-sensitive avian dispersers.

• Fruit and seed mechanical protection is measured in three ways: puncturing resistance using instruments described by Kinzey & Norconk (1990), crushing resistance (e.g., Kinzey & Norconk 1993), and typology of external fruit resistance described by Sabatier (cited in Julliot & Sabatier 1993). The first two methods are the most reliable and should be chosen according to feeding behavior of studied frugivores.

• Chemical composition of fruit measures frugivore reward, generally in terms of dry weight of protein, lipid and carbohydrate (e.g., Foster & McDiarmid 1983, Howe & Westley 1988). Few studies analyze the importance of secondary compounds in fruit pulp, but see Barnea et al. (1993) for saponins, flavonoids and cyanogenic glycosides, Kreuger & Potter (1994) for saponins and tannins, and Barton et al. (1993) and Barton & Whiten (1994) for protein and fiber content, total phenolics, condensed tannins, and alkaloids. Standards for tannin analysis are recommended by Hagerman & Butler (1989). Sugar-tasting ability has been studied experimentally in forest birds by Levey (1987b), and in

frugivorous primates (e.g., Simmen 1992). Similar experiments have been conducted on taste preference using flavored artificial fruits by Sorensen (1983), and on pulp lipids (Stiles 1993). Herbst (1988), Martinez del Rio & Restrepo (1993), and Martinez del Rio (1994) reviewed nutritional ecology, more particularly for lipids and sugars in fruit-eating birds and bats.

• Several hypotheses can be invoked to explain the evolution of fruit color (Willson & Whelan 1990). Colour measurement should not rely on subjective assessments, nor on methods which rely upon human vision, and should be conducted using a field portable spectroradiometer (Endler 1990), adjusted for the spectral sensitivity of the animals in question (e.g., Burkhardt 1982, Bennett *et al.* 1994, Maier 1994, Regan *et al.* in press). Because the appearance of a color patch depends upon ambient light, which is highly variable in forests (Endler 1993, 1997), ambient light and reflectance of visual background should be taken into account to evaluate color signal conspicuousness. Visual systems of frugivores should also be considered in studies of coadaptation or coevolution with fruit color (e.g., Regan *et al.*, in press). Phenological studies should also monitor the evolution of fruit and infructescence colors with ripening, and take into account multicolored fruits and fruit flags (Stiles 1982, Fuentes 1995).

• Odor and texture should be monitored throughout ripening, although no standard method appears to be used.

Fruiting phenology. It is monitored on annual cycles using one of two protocols: series of standardized censuses conducted along transects (e.g., Gentry & Emmons 1987), and inspection of individually marked plants (e.g., Frankie *et al.* 1974, Opler *et al.* 1980, Wheelwright 1986). Protocols designed to evaluate standing crop can also be applied to fruiting phenology. The classification system of Newstrom *et al.* (1994) provides a logical framework for quantitative description of complex phenological behavior of tropical plants. Patterns are separated at each level of analysis so that adding the time series at each time interval at one level produces a time series pattern for the next higher level. Study levels are hierarchically arranged: individual fruit, infructescence, branch, branch complex, individual plant, population, community, guild, ecosystem. Duration, amplitude, synchrony, cycle, interval, regularity, seasonality, and frequency are used to describe fruiting phenology.

Studies of adaptive significance and consequences of fruiting phenology for primary consumers. They have been reviewed by van Schaik *et al.* (1993). Complementary research on consequences of fruit shortage has been conducted on marsupials by Atramentowicz (1982), on birds by Worthington (1982), and on primates by Peres (1994). Worthington (1982) probably used the most detailed protocol to measure the effect of food supply on breeding rhythm and population size of frugivorous birds on an island. It requires a precise definition of diet, availability of food resources in energetical terms, and energetic demand for breeding activity of the whole bird population.

Protocols for the assessment of fruit abundance and standing crop. They have been reviewed by Blake *et al.* (1990), and evaluated by Stashko & Dinerstein (1988) for bats, and by Chapman & Wrangham (1994). Phenology transects or quadrats, each ideally including only one habitat type, are used to assess nature and size of fruit crops by visual estimation using a relative rank, extrapolation from fruit counts of canopy subsections (see Chapman *et al.* 1992), or derivation from DBH or crown volume. Exhaustive monitoring of fruiting resources is possible only when dispersers have small ranges. Phenological studies and relative estimation of fruit abundance by fruit fall along trail systems are usually not helpful in the estimation of fruit density. Zhang & Wang (1995) compared relative advantages and disadvantages of fruit-trap collection, platform observation, and racked-ground survey. Any of the three methods can be used for the approximation of annual fruiting phenology, but that of fruit-trap collection is best able 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 during fruit scarcity, collection of dropped, less preferred, or damaged fruits, underestimation of slow-ripening or seasonally-ripening 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 completion, focal-animal sampling, sampling all

occurrences of some 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 computerized data recording and analysis, such as The Observer system (Visser 1993, Wawra 1994). For a review of behavioral data collection methods and equipment, see Lehner (1996).

Frugivore 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 frugivore activity independently of time. Observation of frugivore behavior at fruiting trees 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., Daily & Ehrlich 1994). When using bioenergetic 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 plant requires measuring the accessibility of fruit to frugivores and analyzing feeding behaviors. Specific identification of dispersers is important to separate mashers, dropping many seeds under the parent tree, from gulpers, ingesting fruit whole (Levey 1987a). Categories of fruit-handling behavior have been described by Levey (1986) and Foster (1987).

Defining food choices and diets. Different methods are used to define diets: direct visual recording (e.g., Hladik 1977), which provides detailed information but is practicable only when conditions of visibility are excellent; stomach content, and time spent feeding (Clutton-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 Hladik (1977). The frequency method overestimates occasional or short consumption, but is considered as giving similar results as time budget measurement in particular species (Struhsaker 1975, Clutton-Brock 1977). Direct observation,

examination of faeces (e.g., Levey 1986, Julliot & Sabatier 1993) and examination of regurgitation content, are often combined to define diets (e.g., Worthington 1982, Thomas 1988). Advantages and disadvantages of using faecal samples to determine diets of birds has been discussed by Wheelwright *et al.* (1984) and Loiselle & Blake (1990). In birds, diet can also be determined by forced flushing or by forced regurgitation, methods whose efficiencies have been compared by Poulin *et al.* (1994). Analysis of stomach content is still practised on hunted animals (Guillotin *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 & Fleming (1986), and Fleming & Estrada (1993). Efficient seed dispersal requires seeds to escape from their parent tree (Janzen 1970, Connell 1971), and to colonize a site appropriate for germination and further development of seedling (Howe & Smallwood 1982). Schupp (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 waste during exploitation of fructifications (e.g., Howe 1980, Jordano 1983, Becker & Wong 1985, Sun *et al.* 1997). Behavioral differences should be carefully extrapolated, because seed treatment may relate to geographic variability of key plant resources (Gautier-Hion *et al.* 1993).

• Estimating the eventual positive impact of seed consumers and secondary dispersal (specific marking of fruits and seeds which will be scatter-hoarded 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 Davidson *et al.* (1985). For relative roles of monkeys, rodents, and dung beetles, see Estrada & Coates-Estrada (1991). For protocols on myrmecochory, see Horvitz & Beattie (1980), Hughes & Westoby (1990, 1992), Kaufmann *et al.* (1991), Byrne & Levey

(1993), Kaspari (1993), Levey (1993), Levey & Byrne (1993), and Horvitz & Schemske (1994). Secondary seed dispersal has also been demonstrated in earthworms (Willems & Huijsmans 1994), fish (Gottsberger 1978, Goulding 1980, Kubitzki & Ziburski 1994, Souza-Stevaux *et al.* 1994), reptiles (Rick & Bowman 1961, Dawson 1962, Côrtes Figueira *et al.* 1994), and large ground vertebrates (e.g., Rodrigues *et al.* 1993, Feer 1995). Differentiating seed predation by vertebrates and invertebrates is usually done with seed exclosures (e.g., Terborgh *et al.* 1993). Transport of seeds by food-hoarding animals has been studied with radioactively-labeled seeds, radio-tagged and metal-tagged seeds (Price & Jenkins 1986), coded thread passed through seeds (e.g., Forget 1990), or recovery of marked large seeds (e.g., Mack 1995). Van der Wall (1990) reviewed studies of seed dispersal in fruit-caching 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-predatory insects by frugivores. For studies investigating insect survival after passage of ingested seeds through bird guts and their dissemination by frugivores, see Nalepa & Piper (1994) and Guix & Ruiz (1995).

• Measuring digestive transit time and assimilation efficiency as adaptation to frugivory has been studied by Worthington (1989) and Bosque & Parra (1992) on tropical birds. Paper layers (Levey 1986), or colored and radio-opaque markers are used to monitor intestinal transit (e.g., Herrera 1984, Milton 1984, Jordano 1987). Karasov & Levey (1990) used ^{3}H-labeled fruits for measurement of transit time, *in vitro* 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, Fleming 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., Théry & Larpin 1993, Julliot 1997, Krijger *et al.* 1997).

• Quality of seed dispersal has been studied by observation and experiment (e.g., Howe 1977, 1993 and previous papers on dispersal of *Virola nobilis*), and/or a modeling approach (e.g., Horvitz & Schemske 1986, Murray 1986, 1988, Martinez-Ramos & Alvarez-Buylla 1995). Other methods include comparing seed rain, seedling and tree communities (e.g., Martinez-Ramos & Soto-Castro 1993, Julliot 1997), evaluating mean dispersal distance by direct observation (e.g., Julliot 1996), comparison of transit time and distance traveled (Sun *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 relationships and dispersal quality. They suggest combining observation and experiment, taking into account complexities of recruitment, and manipulating 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 faeces and uneaten seeds taken from fruits collected in or under trees visited by frugivores. Two criteria are usually taken into account to determine the effect of endozoochory on seed germination: germination rate and speed (Hladik & Hladik 1969, Estrada & Coates-Estrada 1984, Idani 1986). Similar studies have been conducted on seeds whose aril has been removed by ants (Horvitz & Beattie 1980).

• Ultimately, the effect of seed dispersal by frugivores is measured through plant population genetic structure (e.g., Hamrick & Loveless 1986, Hamrick et al. 1993, Alvarez-Buylla & Garay 1994, Carsey & Tombak 1994, Fleming & Sosa 1994, Hall *et al.* 1994).

Documentation of fruits, seeds, and frugivores. This should be managed through standardized databanks including color photographs.

PRACTICAL SUGGESTIONS FOR DATABASE IMPLEMENTATION

General considerations. The topics "pollination" and "seed dispersal" can be looked upon as part of what is called "plant-animal interaction" (PAI). We will use this broader term in this context and in the entity-relationship diagram given in Fig. 2. Databases designed for PAI data should be implemented so that they can be used for storing both complete and published data and, as a working database, for storing incomplete and "raw" field data. This point has considerable 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
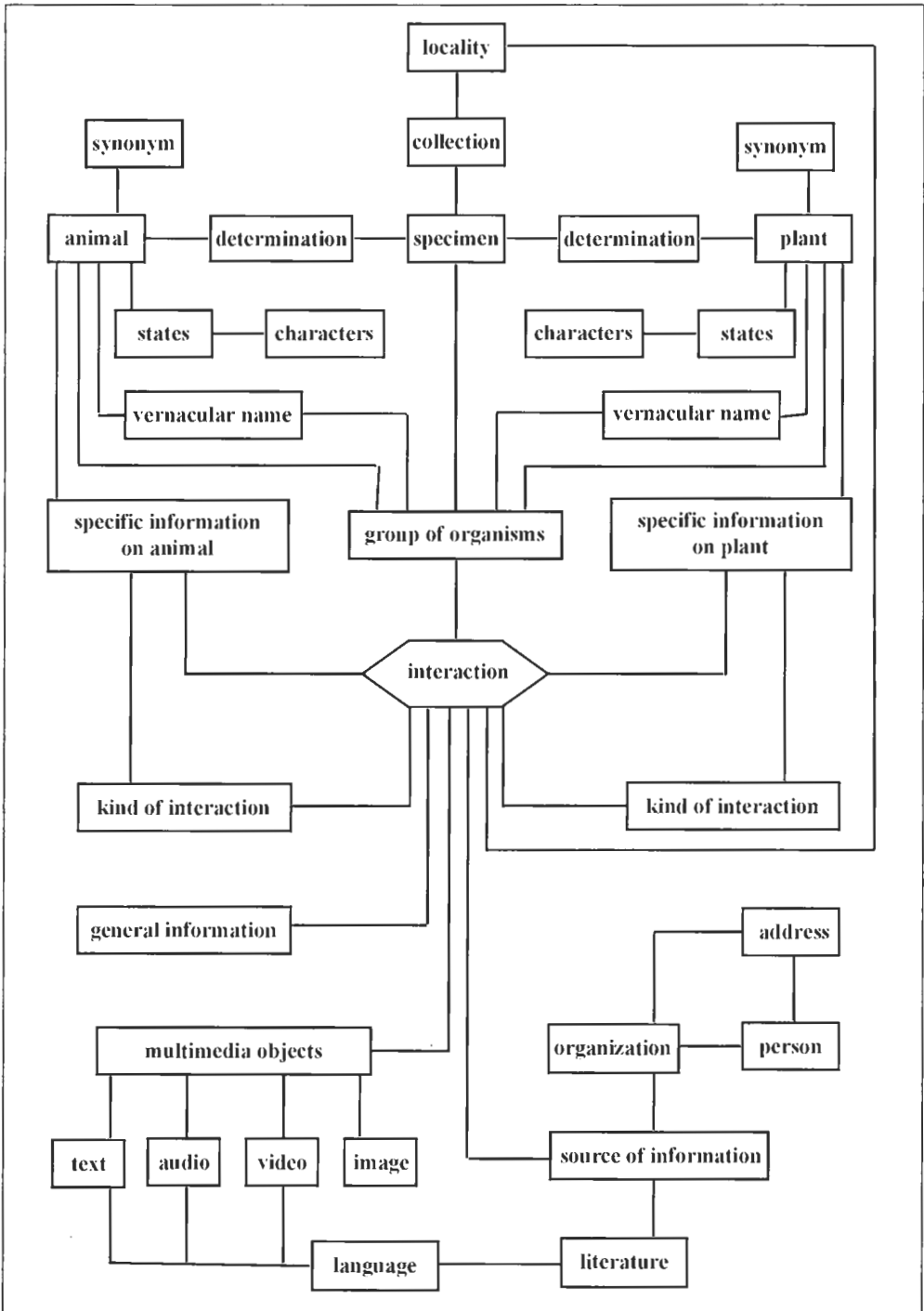
FIG. 2. Entity-relationship diagram for plant-animal interactions.

"worst" case would be that the only data present at time of first data entry is that "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 locality 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 determinations 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 histological 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 synonym has to be changed once and not the determination of all voucher specimens separately.

The data on an observation are texts (text), which is the simplest case in technical 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 / the character "number of stamina" can either be seen as typical for a plant, and thus be unrelated to the observed interaction, or considered as dependent on or important for the observed interaction, 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 hierarchical list (kind of interaction). The key words categorize the entered data with the appropriate terms, e.g., melittophily, endozoochory, frugivory, and so on and

describe, for example, the parts of the animal (e.g., tarsus, antenna) and plant (e.g., leaf, flower, stamen) 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 entity general information refers to all abiotic factors at a certain locality like wind speed, wind direction, temperature, and humidity.

Existing standards. Existing biological and zoological standards and protocols should be used. There are different standards for database structure, data characterization, and data exchange formats. Wherever possible the standards developed by the International Working Group on Taxonomic Databases for Plant Sciences (TDWG) should be used for the botanical contents (Bisby 1995).

Modeling of collection data can be done according to the ASC (ASC 1993) and/or the CDEFD (Behrendsohn *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 HISPID (Croft 1992) and POSS standard (Gillet *et al.* 1995).

Characterization of plant parts can be done according to the TDWG Standard of Economic Botany Data Collection Standard (Cook 1995, for an implementation see Boos & Hoppe 1996). It contains a master list of plant parts which must be completed by adding missing plant parts if necessary. The World Geographic Scheme for Recording Plant Distributions (Hollis & Brummit 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 database systems can be carried out with the XDF format (Allkin & White 1988). A simpler data exchange can be done via flat files whenever possible, particularly for import of data from spreadsheet programs or when exporting data to statistical programs. Further standards exist for plant names (Brummitt & Powell 1992) and herbarium acronyms (Holmgren *et al.* 1990).

New standards. A hierarchical system of key words for the characterization of interaction data (kind 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 seed

dispersal, and then for all other types of interactions. This list will then be presented to the TDWG for discussion. The same applies for characters and their states in specific information on animal / plant.

Implementations. An implementation of the entity relation diagram described above is currently being carried out as a part of the systematic and taxonomic database system SysTax (Hoppe *et al.* 1989, 1996; Kümmel 1989; Boos 1992, 1996; Hoppe & Boos 1996; URL: http://www.biologie.uni-ulm.de/systax/). At the SysTax WWW site the latest version of the keyword list (kind of interaction) and character list (specific information on animal/plant) will be published for further discussion. All those scientists working on pollination and seed dispersal are encouraged to collaborate in designing and improving these standards. A WWW query form will admit at least simple queries for interacting organisms. For a more complex data analysis, however, the tools for the underlying database management system have to be used.

Any implementation of a database system for PAI data should also allow for export of a subset of data typical for a certain country or any other region of interest. A small "database" with the inventory of taxa and their characters and pictures of seeds, fruits, and frugivores can then be made accessible both via internet connection or on CD-ROM. The data can be accessed by any WWW browser or through the programs of the DELTA package (Dallwitz *et al.* 1992) which allow an interactive determination of organisms together with pictures of the taxa and their characters.

ACKNOWLEDGMENTS

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