Structural Variation

Diversity is great in the internal and external structure of seeds. This diversity is related primarily to the wide range of methods of dispersal and germination. The morphological variations include differences in size, form, texture, color, and presence or absence of special structures such as arils of exostomic (elaiosome, caruncle), raphal (strophiole), or funicular origin (Boesewinkel and Bouman 1984, Flores 1999). Anatomical variations include the presence, absence, or position of the storage tissues; the size, form, and position of the embryo; the form and size of the chalazal zone, and the structure of the seedcoat.

The size and position of the embryo vary among seeds (Bernhardi 1832). The area occupied by the embryo is inverse to that used by the endosperm, perisperm, or both. A larger embryo has a smaller endosperm or perisperm, and vice versa. The classification system in this chapter is based on the size, position, and form of the embryo. It represents a modification of the classification system proposed by Martin (1946). Although some types overlap, the taxonomic usefulness of the classification is maintained (Duke 1969). Types must be identified immediately after fruit dehiscence, especially in seeds with no maturation drying where embryo development is continuous. For example, in *Virola koschnyi* seeds, the foliaceous, haustorial, and divergent cotyledons begin to develop inside the seed after seed dispersal, and because space is limited the cotyledonar blade folds (Flores 1992c). In *Compsoneura sprucei* the cotyledonar development is faster and the foldings are more conspicuous.

The following classification system divides seed embryos into three primary types: basal, peripheral, and axile. Basal is further divided into four subtypes and axile into seven (fig. 95).

Basal Embryos

Embryos are usually small, nonperipheral, and restricted to the inferior half of the seed, except in the lateral type. The seeds are medium to large, with abundant endosperm, starchy or oily. The rudimentary and broad subtypes are found in the monocotyledons and dicotyledons; the capitate and lateral subtypes are typical of the monocotyledons (fig. 95).

(1) Rudimentary: The embryo is small and globular to oval-oblong. Cotyledons are rudimentary or obscure, sometimes evident, simulating miniatures of the linear or spatulate types; e.g., *Ilex skutchii* (Aquifoliaceae), *Calatola costaricensis* (Icacinaceae), *Magnolia poasana* (Magnoliaceae), *Compsoneura sprucei*, *Myristica fragrans*, *Otoba*, *Virola* (Myristicaceae), *Minquartia guianensis* (Olacaceae).

(2) Broad: The embryo is as wide or wider than it is high, and very fleshy. It could be globular or lenticular, peripheral or nearly so. This type is common in dicotyledons and monocotyledons that are quite primitive, aquatic, marshy, or parasitic.

(3) Capitate: The embryo expands distally into a head-like form (turbinate); e.g., *Tradescantia* (Commelinaceae), *Dioscorea* (Dioscoreaceae).

(4) Lateral: The embryo is basal-lateral or lateral, inclined to expand in the plane of the periphery. The embryo is usually less than one-half of the seed (inferior half) but can be larger. Typical in Poaceae.

Peripheral Embryos

Embryos are usually elongated and large. The embryo occu-

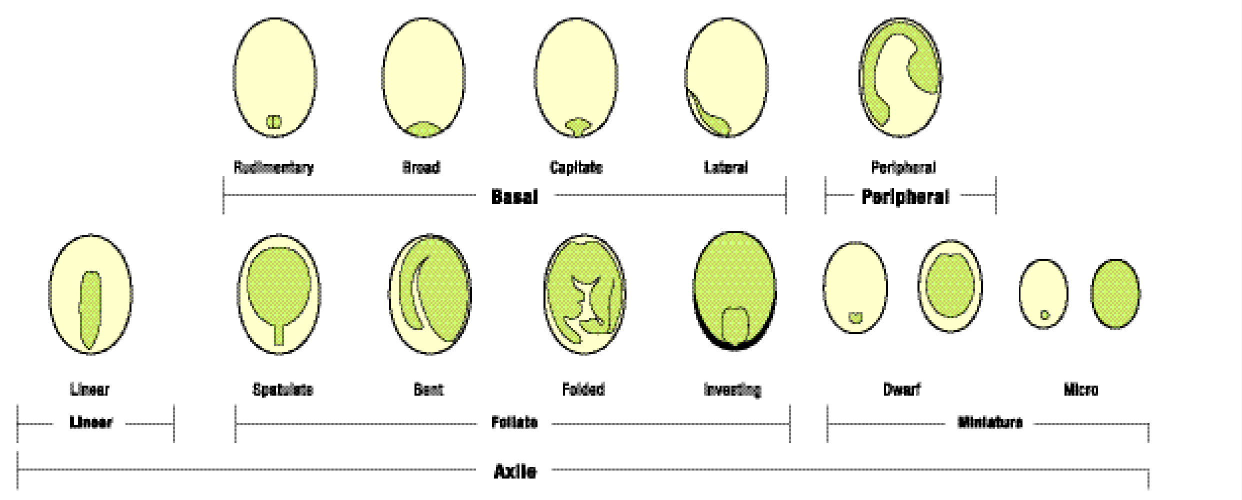

Fig. 95. Seed types and embryo position.

(Redrawn from Martin. 1946).

pies one-quarter to three-fourths of the seed (fig. 95). It is partially contiguous to the seedcoat and often curved, central or lateral, with cotyledons narrow or expanded. The endosperm or perisperm is starchy. As is typical in dicotyledons, one cotyledon can be smaller or abortive (*anisocotyly*); e.g., *Pereskia* (Cactaceae).

Axile Embryos

Embryos range from small (occupying only part of the seed's lumen) to large (occupying the whole lumen), central (axile), straight, curved, coiled, bent, or folded (fig. 95). The endosperm can be oily or starchy. Found in gymnosperms, dicotyledons, and monocotyledons.

(1) Linear: The embryo is usually several times longer than it is wide. It can be straight, curved, or coiled. The cotyledons are small, not expanded or not developed. Seeds are not minute. Examples include *Annona* (Annonaceae), *Tovomita*, *Tovomitopsis*, *Garcinia intermedia* (Clusiaceae), *Elaeocarpus*, *Sloanea* (Elaeocarpaceae), *Muntingia calabura* (Tiliaceae), *Garrya laurifolia* (Garryaceae), *Bertholletia excelsa*, *Eschweilera*, *Lecythis* (Lecythidaceae), *Ardisia brenesii* (Myrsinaceae), and *Zizyphus* (Rhamnaceae).

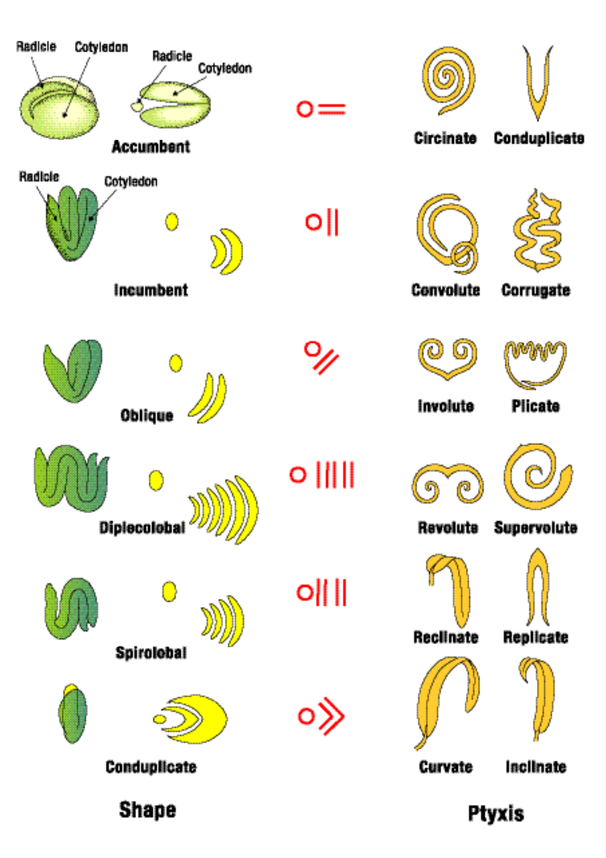

Fig. 96. Embryo shapes and cotyledonar ptyxis.

(2) Miniature: Embryos stocky or minute in small-to-minute seeds. Seedcoats are delicate, often reticulate; the endosperm is not starchy. Two types exist:

(a) Dwarf: The embryo is variable in relative size, small to total (whole seed lumen). It is commonly oval, elliptic, or oblong, with incipient cotyledon development. The embryo is frequently stocky. Seeds are small at 0.3 to 2.0 mm long; e.g., *Clethra* (Clethraceae), *Buddleja americana* (Loganiaceae), several Ericaceae.

(b) Micro: The embryo is minute or total (whole seed lumen), globular, and usually undifferentiated. Seeds are small, commonly less than 0.2 mm long; e.g., Orchidaceae.

(3) Foliate: The embryo is large, one-fourth to all of the seed lumen, central rather than peripheral. Cotyledons are expanded and the endosperm is not starchy. Seeds are medium to large. Four types exist:

(a) Spatulate: The embryo is straight, and cotyledons are variable, from thin to thick and from expanded to broad; e.g., *Aspidosperma*, *Tabernaemontana* (Apocynaceae), *Bixa orellana* (Bixaceae), *Cornus disciflora* DC. (Cornaceae), *Diospyros* (Ebenaceae), *Hyeronima*, *Sapium* (Euphorbiaceae), *Casearia*, *Xylosma* (Flacourtiaceae), *Cedrela*, *Melia azedarach* (Meliaceae), *Genipa americana*, *Simira maxonii*, *Psychotria* (Rubiaceae), *Zanthoxylum kellermanii* P. Wilson (Rutaceae), *Manilkara zapota*, *Chrysophyllum cainito* (Sapotaceae), *Goethalsia meiantha* (Tiliaceae), *Guajacum sanctum* (Zygophyllaceae).

(b) Bent: The embryo is bent and spatulate and usually has thick cotyledons, planoconvex, bent on the hypocotyl (fig. 96). The latter is partially immersed in the area of cotyledon overlapping. In the most common type, the curvature occurs in the plane of the cotyledons [(o =), accumbent, pleurorhizal]. The curvature also can be against the cotyledonar plane (o |), incumbent, notorhizal; or can be oblique (o //) if it is intermediate between accumbent and incumbent. The fourth subtype is the orthoplocal: the cotyledons are incumbent and conduplicate (o >>) as seen in *Avicennia*. The spirolobal embryos (o | |) have incumbent cotyledons, folded once, while diplecolobal embryos have two or more folds (o | | |). The convolute cotyledons are present in *Terminalia* (Duke 1969). Examples include *Acer pseudoplatanus* (accumbent, Aceraceae), *Ceiba pentandra* (bent, Bombacaceae), *Crataeva religiosa* (spirolobal, Capparidaceae), *Caryocar costaricense* (accumbent, Caryocaraceae), *Sapindus saponaria* (Sapindaceae), *Ficus*, *Maclura tinctoria* (bent, Moraceae), and *Myrcianthes fragrans* (accumbent, Myrtaceae).

(c) Folded: The embryo has thin cotyledons, expanded and folded in several ways (fig. 96). Embryos with conduplicate cotyledons are frequent in Sapindales and Malvales (Duke 1969). In Vochysiaceae, the cotyledons are foliaceous, large, and convolute as seen in *Vochysia*, *Qualea*, and *Calycanthus occidentalis* (Calycanthaceae) (Corner 1976; Flores 1993a, 1993b). Examples of folded embryos include *Bursera simaruba* (L.) Sarg. (Burseraceae), *Couratari*, *Couroupita* (plicate; Lecythidaceae), *Tilia americana* (Tiliaceae), *Myrcia splendens* (conduplicate; Myrtaceae), and *Pimenta guatemalensis* (involute; Myrtaceae).

(d) Investing: The embryo is erect; the cotyledons are thick, overlapping, and encase a small hypocotyl. The endosperm is missing or very reduced. The embryo may be confused with bent or spatulate embryos. It can be associated with cryptocotylar seedlings. Examples include *Alnus acuminata* (spatulate-investing; Betulaceae), *Calophyllum brasiliense* (Clusiaceae), *Prioria copaifera* (Fabaceae-Caesalpinioideae), *Pentaclethra macroloba* (Fabaceae-Mimosoideae), *Dipteryx oleifera* (Fabaceae-Papilionoideae), *Quercus* (Fagaceae), *Ocotea*, *Nectandra* (Lauraceae), *Carapa guianensis*, *Guarea* (Meliaceae), *Nephelium lappaceum*, *Cupania* (Sapindaceae), and *Quassia amara* (Simaroubaceae). The total or partial fusion of the cotyledons along the adaxial surfaces is common in seeds with cryptocotylar germination such as *Calophyllum*, *Carapa*, and *Guarea* (Flores 1994c, 1994g).

RELATIONSHIPS BETWEEN SEED STRUCTURE AND STORAGE BEHAVIOR

Some seeds lose water during maturation drying and gradually acquire tolerance to desiccation, while others maintain a high water content, do not experience a reduced cellular metabolism, and are sensitive to desiccation and temperature decreases. The tolerance/intolerance to desiccation shown by the seeds in their natural environment is also exhibited when they are stored.

Sensitivity to desiccation limits a seed's storage potential, genetic conservation, and use in trade. Roberts (1973) defined two types of seeds based on sensitivity to desiccation: orthodox seeds (those that undergo maturation drying) and recalcitrant seeds (those that do not undergo maturation drying).

The ability to tolerate desiccation by orthodox seeds is associated with metabolic changes such as respiration decrease, increase of some carbohydrates or oligosaccharides, and accumulation of dehydrines (LEA proteins). During germination the seeds lose this tolerance, frequently several hours after radicle protrusion. Dehydration at this stage leads to irreversible damage, in which the peroxidation of lipids and free radicals has an important role (Côme and Corbineau 1996a, 1996b; Finch-Savage 1996). However, mature orthodox seeds can be dehydrated without damage to very low levels of moisture (1 to 5 percent) and in a variety of conditions (Kermode 1997). Bound water (structural) is less easily frozen than free water. Bound water seems to be a crucial component to tolerating desiccation, and in the orthodox seeds all water is bounded (Leopold and Vertucci 1986, Leopold and others 1992). In storage, the longevity of seeds increases with a reduction of the water content in a predictable and quantifiable manner. Bonner and Vozzo (1990) subdivide these seeds into (a) true orthodox, which "can be stored for long periods at seed moisture contents of 5 to 10 percent and subfreezing temperatures" and (b) suborthodox, which "can be stored under the same conditions, but for shorter periods due to high lipid content or thin seedcoats."

Recalcitrant seeds are rich in free water and neither tolerate nor survive desiccation. They die when the water potential reaches levels similar to those of permanent withering in many growing tissues (-1,5 to 5,0) (Pritchard 1991, 1996). The dehydration of intolerant tissues (recalcitrant) provokes membrane deterioration (plasmalema and mitochondria), protein denaturalization, and reduction of both the respiratory rate and the ATP level (Leopold and others 1992). The oxidative processes and the free radical seem to be involved in cellular and molecular deterioration (Côme and Corbineau 1996a, 1996b). The seeds show a strong resistance to rehydration and the loss of cellular integrity leads to a loss of viability. Recalcitrant seeds are present in at least 70 percent of tropical trees. Their sensitivity to temperature lowering is due to the high water content.

Because some seeds did not fit readily into either orthodox or recalcitrant categories, Ellis and others (1990a) proposed a third category: the intermediate seeds. These seeds survive desiccation at intermediate moisture levels but not to the degree of orthodox seeds. This last category can be considered arbitrary, and the existence of a recalcitrance gradient throughout the different species has been suggested (Finch-Savage 1996, Flores 1996).

Variations in the sites of water storage and the gradual damage observed in the seed's tissues when it dehydrates, can be illustrated by the seeds of the following species: *Calophyllum brasiliense* (Clusiaceae), *Otoba novogranatensis* (Myristicaceae), *Minquartia guianensis* (Olacaceae), *Caryocar costaricense* (Cary-

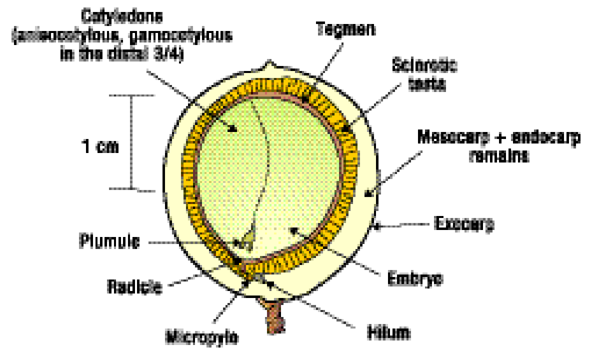

Fig. 97. Berry of *Calophyllum brasiliense* enclosing the overgrown seed, (longitudinal section).

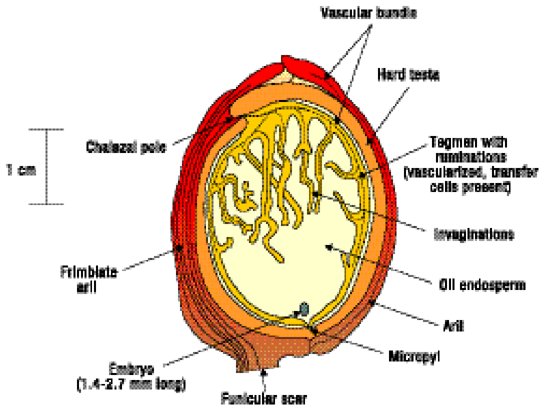

Fig. 98. Seed of *Otoba novogranatensis*, (longitudinal section).

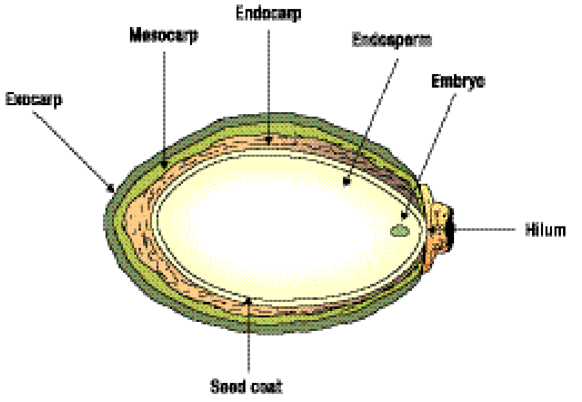

Fig. 99. Drupe of *Minquartia guianensis* enclosing the seed.

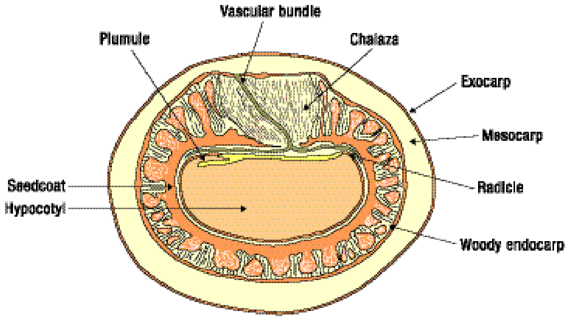

Fig. 100. Drupe of *Caryocar costaricense* enclosing the seed.

ocaraceae), and *Lecythis ampla* (Lecythidaceae) (figs. 97-101, Table 1).

How does dehydration affect seeds? In *Calophyllum brasiliense* the seedcoat is hard and resists desiccation; water loss is slow. Once the seedcoat dehydrates, the water loss directly affects the embryo, with the exposed radicle being the most rapidly affected. The thick cotyledons enclose the small plumule and it dehydrates last. In species with minute, rudimentary embryos (*O. novogranatensis*, *M. guianensis*), the sequence of dehydration is seedcoat ₵ peripheral endosperm and radicle ₵ remaining embryo ₵ inner endosperm. Seed viability deteriorates rapidly upon embryo dehydration. *Otoba novogranatensis* is more sensitive to desiccation than *Minquartia guianensis*, due to endosperm rumination and tegmen vascularization. *Caryocar costaricense* has a curved, accumbent embryo and the plumule and radicle dehydrate immediately after endo-

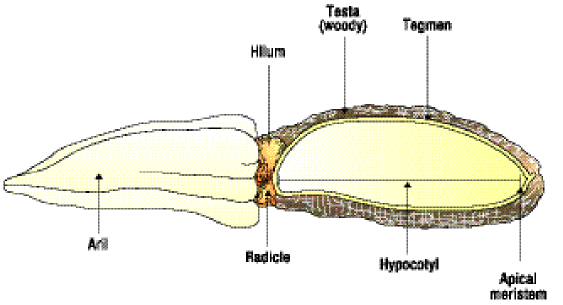

Fig. 101. Seed of *Lecythis ampla* (longitudinal section).

Table 1

Structural variation of five recalcitrant seeds from neotropical species during seed dispersal

	Species				
Structure	*Calophyllum brasiliense*	*Otoba novogranatensis*	*Minquartia guianensis*	*Caryocar costaricense*	*Lecythis ampla*
Fruit	Berry	Septicidal Capsule	Drupe	Drupe	Pyxidium
Type of diaspore	Fruit	Seed	Fruit	Fruit	Seed
Endocarp surrounding the mature seed	Soft, thin, crushed	Absent	Drupe, hard endocarp	Drupe, hard endocarp	Absent
Seedcoat	Hard	Hard	Soft	Papyraceous	Hard
Testa	Hard	Hard	Soft	Soft	Hard
Tegmen	Thin, soft	Thin, ruminate	Soft, fragmentary	Thin, soft	Remnants
Endosperm	Absent in mature seed	Massive, nuclear-cellular	Massive, cellular	Absent in mature seed	Absent in mature seed
Perisperm	—	—	—	—	—
Embryo	Massive, complete	Minute, rudimentary	Minute, rudimentary	Massive, complete	Massive, undifferentiated
Cotyledons	Massive, fused	Differentiate and develop during germination	Differentiate and develop during germination	Small, scaly	Differentiate and develop during germination, small, scaly
Hypocotyl	Thick, massive	Differentiate and develop during germination	Differentiate and develop during germination	Thick, massive	Thick, massive
Epicotyl	Very small	Differentiate and develop during germination	Differentiate and develop during germination	Very small	Differentiate and develop during germination
Radicle	Thick, small	Differentiate and develop during germination	Differentiate and develop during germination	Thick, small	Rudimentary
Reserves location	Cotyledons, hypocotyl	Endosperm	Endosperm	Hypocotyl	Hypocotyl
Water storage	Whole embryo	Mainly endosperm	Mainly endosperm	Hypocotyl	Hypocotyl

carp dehydration. The dehydration of *Lecythis ampla* seeds first affects the seedcoat and then the meristematic poles (radical and apical); they die instantly after seedcoat dehydration.

The seeds enclosed in berries (*C. brasiliense*) or drupes (*C. costaricense*, *M. guianensis*) are protected by the pericarp tissues, which help maintain seed moisture. In these cases, the functional unit is the fruit and dehydration is slower.

The moisture level below which a seed loses its viability varies from one seed to another. Variations are found among seeds collected from the same tree as well as from different trees, zones, seasons, or years. The recalcitrant behavior seems to be genetically determined and its genetic base is still not well understood. The variations found can be explained if the seed history from flower inception to seed dispersal and germination is analyzed carefully (Flores 1994i, 1996).

The difference found between temperate and tropical recalcitrant seeds must be added to the gradient found in recalcitrance manifestation. Bonner and Vozzo (1990) established two categories: temperate recalcitrant seeds and tropical recalcitrant seeds. The first cannot be dried but can be stored for 3 to 5 years at near freezing temperatures; the latter cannot be dried and are killed by temperatures below 10 to 15 °C, depending on the species.

Unfortunately, very limited information exists on the tissular, cellular, and biochemical alterations produced by dehydration in the recalcitrant seeds, as well as on the appropriate strategies and mechanisms to manage them under storage conditions. The diversity of types found in recalcitrant seeds is preliminary and further complicates the issue. The problem of cellular desiccation is complex; it seems to involve genetic components that lead to mechanisms of cellular protection. These mechanisms limit the cell damage produced by seed dehydration and promote cellular repair, reversing the changes induced by water loss (Kermode 1997). The accumulation of protecting substances in the tolerant tissues is quite possible (Kermode 1997). The dehydrines, disaccharides (sacarose), and oligosaccharides (raffinose and stachyose) may have an important role in the stabilization and maintenance of the

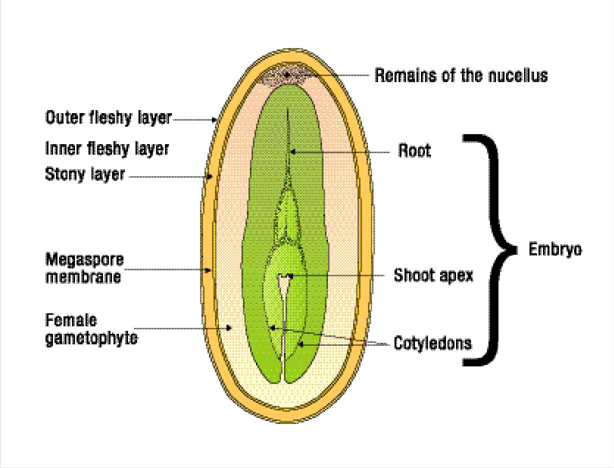

Fig. 102. *Pinus* seed (longitudinal section).

(Redrawn from Foster & Gifford, 1974).

membrane system and other sensitive systems (Kermode 1997, Leopold and others 1992).

THE GYMNOSPERM SEED

The gymnosperm seed initiates with the fertilization of the egg cell. The zygote forms the embryo (2n), which remains immersed in the nutritious tissue (endosperm) of the megagametophyte (n). The integument gives rise to the seedcoat (2n, part of the tissues of the maternal tree).

Embryo Development

The gymnosperms have a phase of free nuclear division in early embryogeny unlike most angiosperms. The exceptions include *Sequoia sempervirens*, *Gnetum*, and perhaps *Welwitschia* (Foster and Gifford 1974, Maheshwari and Vasil 1961). The number of free diploid nuclei varies within species; some cycads may have about 1,000, while *Pinus* has 4 (Foster and Gifford 1974). The free nuclear division phase is followed by a cellular phase in which cell walls are formed and the suspensor, the apical meristem, the radicle, the hypocotyl, and the cotyledons are gradually differentiated.

The mature embryo is linear except in *Ephedra*, although some are slightly spatulate (fig. 102). *Zamia* and *Gingko* have large, expanded cotyledons covering the small embryo axis. The cotyledon number varies among and within the species. Conifers have 3 to 18 small, narrow cotyledons organized in a whorl; for example, *Pseudotsuga* has 4 to 12; *Abies,* 2 to 10; *Tsuga*, 2 to 7; *Thuja, Juniperus,* and *Taxus,* 2 (Chowdhury 1962, Martin 1946). The average in *Pinus* is 8.1 (Butts and Buchholz 1940). In conifers, the embryo may be physiologically mature when seed dispersal occurs, although there are exceptions such as *Pinus cembra*, *P. sylvestris* L., and *Picea abies*. The last has a rudimentary embryo that continues its development if the dispersed seed reaches a suitable environment (Krugman and others 1974, Stokes 1965). Most gymnosperms have a tendency to polyembryony because more than one archegonia can be fertilized. In conifers, certain cells of the incipient embryo can separate and form four or more embryos. Some species show a conjugation of both types of polyembryony, although competition eliminates all embryos except one; this one develops and reaches physiological maturity (Foster and Gifford 1974).

Seedcoat

The seedcoat derives primarily from the chalazal tissue in cycads and pines, and from integumentary tissue or from both chalazal and integumentary tissues in *Gnetum*, *Ephedra*, and cypresses. In Podocarpaceae (*Podocarpus costaricensis*, *P. guatemalensis*, *P. macrostachyus*, and *Prumnopitys standleyi*), the epimatium forms a fleshy covering surrounding the seed; this coriaceous covering has a single crest or umbo (Torres-Romero 1988). The seedcoat of *Gnetum* has three integuments while *Ephedra* and *Welwitschia* have only one (Singh and Johri 1972). The seedcoat may be thin and soft or thick and hard. In *Pinus*, the seedcoat has a layer of sclerenchyma derived from the integument. The fleshy layer degenerates during seed development (Foster and Gifford 1974). Some seeds have mucilage canals (cycads) or resin ducts (*Abies*, *Tsuga*, *Libocedrus*), the contents of which impregnate the seeds, making them sticky (Krugman and others 1974, Singh and Johri 1972). The seeds have wings of different sizes and shapes; these wings sometimes fall off early. However, the seed wings of some species, such as *Taxodium* and *Pinus,* may be persistent (Krugman and others 1974).

Endosperm

In early embryogeny the central part of the nucellar tissue (megagametophytic), called the endosperm, disintegrates and forms the corrosion cavity. The suspensor pushes the embryo into this cavity, where it absorbs nutrients (Singh and Johri 1972). The endosperm disorganizes completely at the end of embryogenesis; only a papyraceous layer remains at the micropylar end. The seed matures in two to three seasons. The content, behavior, and fluctuation of growth regulators are similar to those of the angiosperms (Krugman 1966, Krugman and others 1974). The lipid content in the seeds is high, although carbohydrates and proteins are also present. Some pines contain up to 50 percent lipids stored in the endosperm (Krugman and others 1974, Singh and Johri 1972).

FRUIT AND SEED DISPERSAL

Seed dispersal is one of the critical stages in the life cycle of the species. It transports physiologically independent individuals to the habitat occupied by their parents or to new suitable territories, where the seeds may colonize if environmental conditions are favorable (Howe and Smallwood 1982, Willson 1992). The unit of dispersal receives the generic name of diaspore, propagule, or diseminule, and can be formed by the embryo, the seed, the fruit, or the fruit and associated parts of the modified perianth, the receptacle, or both (Harper 1977, Van der Pijl 1972).

Diaspores can be dispersed in space and time. Dispersal in space is the transport from one site to another, usually far from the parent tree. Dispersal in time is the quiescence or inactivity of diaspores for a variable period of time after which they activate under the action of environmental stimuli, unchaining the germination process (Harper 1977). This dispersal of diaspores from the source (parent tree) and commonly around it is called the seed shadow (Janzen 1971a) (seed = diaspore in this context). The source can be the parent tree or a nucleus of multiple parents. Four processes interact to generate the seed shadow which eventually becomes the seedling shadow: seed production, predation, dispersal and quiescence or dormancy (Janzen and Vásquez-Yáñez 1991). The seed shadow, which can be asymmetrical, is affected by two factors: the relationship of density to distance and the direction of dispersal in respect to the source. The relationship density (seed number)-distance in respect to the source reaches a peak and has a tail; the direction has an important ecological value (Janzen 1971a). Outside the peak, the number of seeds decreases centrifugally and forms a negative exponential curve. Habitat fragmentation and other factors such as the behavior of the dispersal agents, the environment, and the genetic constitution can change the conventional form of the curve (Willson 1992).

The expectation is that the dispersed offspring live and breed, but the seed shadow is modified and reduced by predation, lack of germination, and seedling mortality. In general, the lack of natural enemies (predators, pathogens, parasites, and herbivores), the absence of unfavorable interactions, and the probability of finding a favorable site favor natural dispersal.

TYPES OF DISPERSAL

The dispersal of diaspores can be biotic (zoochorous) or abiotic (azoochorous) and their morphology is related to the method of dispersal. In biotic dispersal the vectors are numerous: invertebrates [flies, dung insects and ants (myrmecochory), earthworms, and snails], herbivorous fish (ichthyochory), marine turtles, lizards and desert iguanas (saurochory), birds (ornithochory), and mammals including human beings (mammaliochory). When the mammals dispersing fruits are rodents, the process is called dyszoochory; if the vectors are bats the process is called chiropterochory. Abiotic dispersal is by wind (anemochory), water (hydrochory) or the tree itself (autochory). The last is achieved by active ballistics (tension generated by the dehydration of hygroscopic tissues), passive ballistics (movements of the seeds enclosed in the fruit), and creeping diaspores and barochory (dispersal by weight) (Carlquist 1966; Flores 1994a; Gautier-Hion 1990; Gottsberger 1978; Howe 1990; Terborgh 1986, 1990; Van der Pijl 1972; Van Roosmalen 1985).

In tropical forests most dispersal is achieved by the vertebrates, which obtain food from the seeds and other edible parts of the fruit. The dominance of zoochorous dispersal has been demonstrated in several places. In the French Guiana and Surinam, 6 percent of the diaspores produced by woody forest trees are dispersed by autochory, 11 percent by anemochory, 9 percent by hydrochory, and 74 percent by zoochory. Most diaspores dispersed by water come from riparian species and are typical in marshes or mangrove vegetation, while those dispersed by wind grow at forest edges. In primary forests, zoochory may increase to 87 or 90 percent (Van Roosmalen 1985). Some investigators consider that zoochorous dispersal in the tropical rain forest is about 80 percent (Croat 1975, 1978; Frankie and others 1974; Gentry 1982, 1993; Levey 1987; Levey and others 1994; Opler and others 1980; Stiles 1985; Willson and Thompson 1982; Willson and others 1989).

Most diaspores are polychorous and their morphology indicates the mechanisms of general dispersal, although an obvious modification does not preclude the existence of alternative mechanisms (Bawa and others 1985a, 1985b; Flores 1992b, 1992c, 1993a, 1993b, 1993c, 1994b, 1994f; Howe and Smallwood 1982). The Fabaceae, for example, are dispersed by birds, bats, rodents, Perissodactyla, Artiodactyla, carnivores, water, skin, feathers, wind, ballistics, or gravity (Howe and Smallwood 1982, Van der Pijl 1972, Van Roosmalen 1985), while the Lauraceae are dispersed by birds, bats, monkeys, rodents, carnivores, fish, gravity, and water (Flores 1999). The specificity of disperser or dispersers is uncommon and most fruits and seeds are used and dispersed by several or many vectors, which may include consumers, commensals, predators, commensals and dispersers, or predators and dispersers.

Biotic or Zoochorous Dispersal

Biotic dispersal occurs in three ways. Dispersal is epizoochorous if the transport of diaspores is passive, external, and occurs through diaspore adhesion to animal skin (hairs) or feathers. Biotic dispersal is synzoochorous when animals, eating part of the seeds but not ingesting them, actively transport the diaspores. This type of dispersal extends to predators who store and bury the seeds, thus providing an opportunity for the survival and germination of some seeds. Dispersal is endozoochorous if the diaspore containing the seed, or the seed itself, is ingested and eventually regurgitated or defecated intact (Gottsberger 1983, Van der Pijl 1972). Zoochorous dispersal requires nutritious tissues (aril, pericarp, testa) in the diaspore, chemical attractants (elaiosomes, stale scent), mimetism (seedcoat coloration), or adhesive structures (viscous materials, hooks) (Howe and Smallwood 1982, Van der Pijl 1972). About 80 percent of the vertebrates (50 percent birds, 30 percent other mammals) feed on fruits (Howe and Smallwood 1982, Janson 1983, Janson and Emmons 1990, Levey and others 1994, Terborgh 1986). The most common types of biotic dispersal are described in the following paragraphs.

Ornithochory

Birds have a poor olfactory sense and very well developed vision. To be dispersed by birds, diaspores must have an edible part with an agreeable taste, external protection against premature ingestion, embryo protection (a hard seedcoat, hard endocarp, or both), attractive colors, and a fixed position. The fruits or seeds dispersed by birds are odorless, small, and usually spherical or oval (Levey 1987, Levey and others 1994, Morden-Moore and Willson 1982, Sorensen 1983, Van der Pijl 1972, Wheelwright 1985, Willson and Thompson 1982, Willson and Whelan 1990). Crop size, distance from other fruiting trees, and the nutritious content of other available fruits also affect bird predation and dispersal (Howe 1977, 1981, 1982; Howe and DeSteven 1979; Howe and Richter 1982; Jordano 1983, 1988; Levey and others 1994; Sargent 1990; Stapanian 1982). Nonflying birds also disperse fruits and seeds; for example, the ñandú *Rhea americana* and *Pterocnemia* (Rheidae) and the Tinamidae (*Crypturellus*, *Nothocercus*, *Rhynchotus*, *Tinamus*) feed on fleshy diaspores (Gottsberger 1983, Stiles and Skutch 1989). Parakeets, parrots, macaws (Psittacidae), toucans, and toucanets (Ramphastidae) eat fruits and seeds that can be swallowed entirely. They also split and eat hard fruits that other birds are unable to consume (Gottsberger 1983; Loiselle 1987, 1990, 1991; Loiselle and others 1996; Stiles and Skutch 1989). The Icteridae, Picidae, Trogonidae, Tyrannidae, Turdidae, and Funaridae also feed on fruits (Gottsberger 1983; Loiselle 1987, 1990, 1991; Stiles and Skutch 1989). The following paragraphs describe the fruits birds prefer.

Fruits with bright color (brown, green, yellow, or orange), fleshy but sufficiently dry, with a woody or semiwoody exocarp, a few large seeds, and a fleshy mesocarp rich in lipids are frequently consumed (Janson 1983, Johnson and others 1985, Van der Pijl 1972, Van Roosmalen 1985). The fruits are usually green drupes, berries, or camaras (e.g., many Anacardiaceae (*Astronium*), Burseraceae (pyrenoid drupe in *Protium*, *Tetragastris*, *Trattinickia)* (figs. 72-73), Combretaceae (*Buchenavia*), Clusiaceae (*Calophyllum brasiliense*, *Symphonia globulifera*), Lauraceae (*Aniba*, *Licaria*, *Nectandra*, *Ocotea*, *Persea*) (fig. 70), and Fabaceae-Papilionoideae (*Dipteryx panamensis)* (fig. 52). Specialized frugivorous birds such as toucans, toucanets, caracaras, cotingas, and quetzals consume these fruits (Avila and others 1996; Bonaccorso and others 1980; DeSteven and Putz 1984; Flores 1992a, 1994a, 1994f, 1999; Gentry 1993; Van Roosmalen 1985). For example, 63 percent of the fruits eaten by the quetzal *Pharomachrus mocinno* (Trogonidae) are lauraceous; the remaining 37 percent are the fruits of the Myrsinaceae, Araliaceae, Verbenaceae, Solanaceae, Myrtaceae, Melastomataceae, Moraceae, and Clusiaceae (Avila and others 1996). The quetzal is a highly specialized, frugivorous bird and an excellent disperser of fruits and seeds, especially during the nonreproductive season when it may range over many kilometers (Avila and others 1996).

Drupes and berries with bright color (red, pink, white, black, blue, purple, orange, yellow, or greenish yellow), membranaceous or slightly coriaceous exocarp, fleshy mesocarp, watery, rich in sugars, poor in lipids and proteins, and fast-rotting are highly appreciated by birds (Levey 1987, Moermond and Denslow 1985, Sorensen 1983, Van der Pijl 1972, Van Roosmalen 1985, White 1974). Examples include Anacardiaceae (*Spondias*, *Tapirira*), Araliaceae (*Dendropanax*), Boraginaceae (several species of *Cordia*), Cecropiaceae (*Cecropia*, *Pourouma*), Malpighiaceae (*Byrsonima, Tetrapodenia*), Melastomataceae (*Conostegia*, *Miconia*), Myrsinaceae (*Ardisia*), Myrtaceae (*Eugenia*, *Marliera*, *Myrcia*, *Psidium*, *Syzygium*) (fig. 68), Olacaceae (*Minquartia guianensis*) (fig. 71), Piperaceae (*Piper*), Rosaceae (*Prunus*), Rubiaceae (*Alibertia*, *Coussarea*, *Faramea*, *Genipa*), Solanaceae (*Brunfeldsia guianensis*, *Cestrum*), Simaroubaceae (*Picramnia*), Theaceae (*Symplococarpon*), Ulmaceae (*Trema micrantha*), and Verbenaceae (*Citharexylum mocinnii*), (Flores 1994e, Gentry 1993, Herrera and Jordano 1981, Van Roosmalen 1985).

Dehiscent fruits (follicles, pods, etc.) and seeds with special structures (arils, elaiosomes, caruncles, strophioles, and funicles) or sarcotestas rich in lipids, sugars, or mucilage feed birds. The testas or sarcotestas are usually black, white, red, orange, or yellow and the arils are red, white, yellow, or orange (Van der Pijl 1972, Van Roosmalen 1985). The funicles are fre-

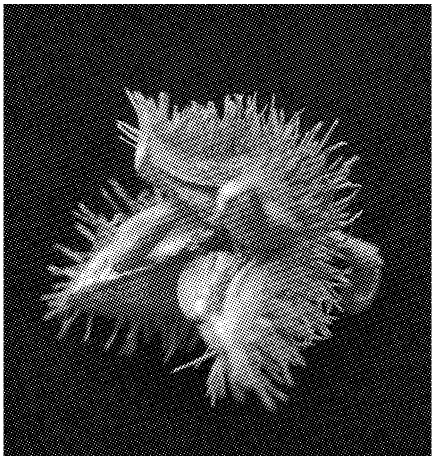

Fig. 103.

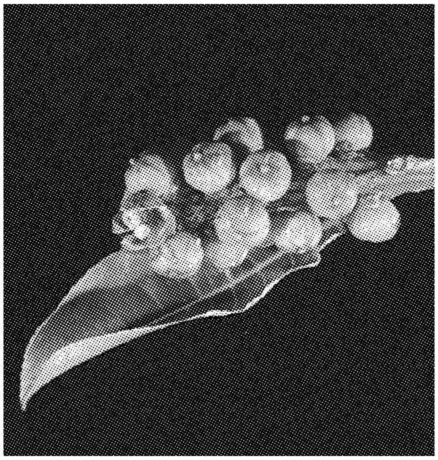

Fig. 104.

Fig. 106.

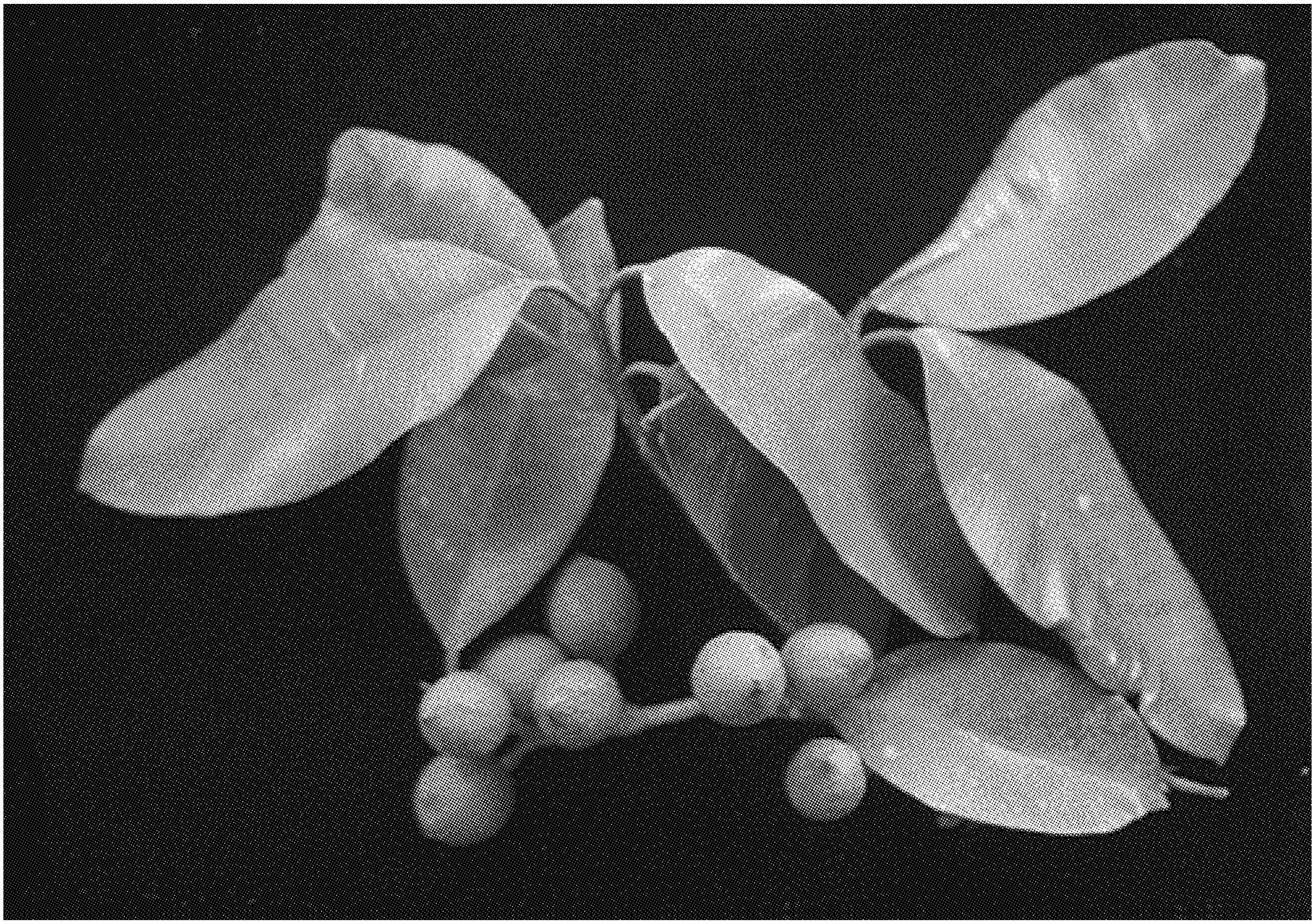

Fig. 105.

quently long and the seeds hang (Van der Pijl 1972). The color of the seedcoat combines with that of the aril and frequently the endocarp and exocarp to create an attractive display eliciting ornithochory. Examples include several Annonaceae (*Xylopia*), Apocynaceae (*Stemmadenia*), Bixaceae (*Bixa orellana*), Fabaceae-Caesalpinioideae (*Dialium guianense*), Clusiaceae (*Clusia*), Connaraceae (*Connarus*, *Rourea*), Dilleniaceae (*Curatella*, *Davilla*), Elaeocarpaceae (*Sloanea*) (fig. 103), Euphorbiaceae (*Sapium*) (fig. 104), Flacourtiaceae (*Casearia arborea*, *C. decandra*, *C. guianensis*), Magnoliaceae (*Magnolia*), Meliaceae (*Guarea*, *Trichilia*) (fig. 56), Fabaceae-Mimosoideae (*Acacia*, *Cojoba*) (fig. 64), Myristicaceae (*Virola*, *Compsoneura*, *Otoba*) (fig. 62), Sapindaceae (*Cupania*) (fig. 59), and Zygophyllaceae (*Guaiacum sanctum*) (Flores 1992c, 1996, 1999; Gentry 1993; Howe 1981; Howe and DeSteven 1979; McDiarmid and others 1977; Van Roosmalen 1985; Wendelken and

Martin 1987). When the follicles of *Xylopia aromatica* open, blue seeds contrasting with the reddish interior of the endocarp are revealed. The sarcotesta of the seeds and the white aril attract different birds which swallow seeds intact (Gottsberger 1993). The black seeds of *Connarus* are partially covered by a yellow, fleshy aril contrasting with the red or orange inner surface of the open follicle; the display attracts birds which swallow or remove the seeds, eating the aril and discarding the seed (Van Roosmalen 1985).

Capsules, nuts, or other types of fruits with fleshy floral structures attached are also preferred. Examples are Moraceae (pseudofruits of *Brosimum*, *Morus*), Ochnaceae (fleshy receptacle in *Ouratea*), and Polygonaceae (succulent perianth tube in several species of *Coccoloba*) (Flores 1996, 1999; Gentry 1993; Van Roosmalen 1985).

Finally, mimetic seeds are swallowed and transported by mistake because the colored exocarp or testa resembles an aril (Howe and Smallwood 1982, Van Roosmalen 1985). Examples include many Fabaceae-Mimosoideae (*Adenanthera*, *Cojoba*), Fabaceae-Papilionoideae (*Erythrina*, *Ormosia*), Meliaceae (some *Guarea* in which the testa imitates a sarcotesta) (Corner 1953).

Numerous birds eat fruits or seeds, digest the mesocarp or the aril, and defecate or regurgitate the seed, which is often surrounded by a hard endocarp. In many cases, the gastric juices scarify the testa, the endocarp, or both, and facilitate the germination of the seeds. The seeds of various species of the genera *Cordia*, *Virola*, *Protium*, *Tetragastris*, *Xylopia*, and others are dispersed in this way (Flores 1992c; Howe 1977, 1990; Howe and Ritcher 1982; Howe and Vande-Kerckhove 1981).

Mammaliochory

Dispersal by mammals is more developed in the tropical zones. The diaspores dispersed by mammals have characteristics similar to those dispersed by birds; other groups, such as bats, often eat the same fruits (Van der Pijl 1972).

Chiropterochory

The presentation of diaspores eaten by bats is similar to or the same as that exhibited by those consumed and dispersed by birds; however, the diaspores dispersed by bats are usually green, brown-yellow, brown, purple, black, or variegated and are found at the ends of the branches. The color is not important because bats are nocturnal and blind to color, but their olfactory sense is well developed. Bats prefer a stale odor and many consume diaspores that have this odor (butyric acid), which is produced by substances in fermentation, usually in the tissues of the fleshy mesocarp (Flores 1994e, 1999; Van der Pijl 1972). The taste of preferred diaspores varies from insipid to acid or sweet, and the consistency is soft to semihard. Bats also consume the arils of the seeds of dehiscent fruits, which are commonly rich in lipids (Flores 1994d). The frugivorous bats of the Paleotropics (tropics of Asia and Africa), which belong to Megachiroptera, are important seed dispersors; in the American tropics, bats are members of the Phyllostomidae (Microchiroptera). The major consumers and dispersors are found in the Subfamily Stenoderminae (*Artibeus jamaicensis*, *A. lituratus*, *Dermanura*, *Sturnira*). Those of the Subfamilies Carollinae (*Carollia brevicauda*, *C. castanea*, *C. perspicillata*) and Glossophaginae (*Anoura*, *Glossophaga*) follow as important dispersers (Fleming 1988; Fleming and Heithaus 1981; Timm and others 1989; Van der Pijl 1957, 1972).

Bats are commensals and, in many cases, dispersers. When fruit size exceeds their transport capacity, bats consume the fleshy mesocarp of drupes and berries, and drop the remaining tissues under the tree crown. Smaller fruits are transported to the feeding and resting roosts where the bats drink the mesocarp juice (Bonaccorso 1979; Bonaccorso and others 1980; Fleming and Heithaus 1981; Flores 1992a, 1994e, 1999; Heithaus and Fleming 1978). The fruits of *Calophyllum brasiliense* (Clusiaceae) (fig. 105), *Ocotea austinii* (fig. 70), and *Minquartia guianensis* are transported to feeding and resting roosts. Frequently, populations of seedlings are found on the ground below the roosts (Flores 1994b, 1994e, 1999).

Bats disperse the diaspores of several species in the following families: Anacardiaceae (*Mangifera indica*, *Spondias*), Annonaceae (*Annona*), Bombacaceae (*Quararibea*), Fabaceae-Caesalpinioideae (*Aldina*, *Cynometra*, *Hymenaea*), Caryocaraceae (*Caryocar*), Cecropiaceae (*Cecropia*, *Pourouma*), Chrysobalanaceae (*Couepia*, *Licania*, *Parinari*), Clusiaceae (*Calophyllum*, *Clusia*) (fig. 105), Lauraceae (*Licaria*, *Nectandra*, *Ocotea*, *Persea*), Lecythidaceae (arils, *Lecythis*, *Eschweilera*, *Gustavia*) (figs. 54 and 106), Fabaceae-Mimosoideae (*Inga*, *Cojoba*) (figs. 64 and 76), Monimiaceae (*Siparuna*), Moraceae (*Ficus*, *Brosimum*, *Maclura*), Myrtaceae (*Psidium*), Olacaceae (*Minquartia guianensis*) (fig. 71), Fabaceae-Papilionoideae (*Andira inermis*, *Cassia grandis*, *Dipteryx*, *Lecointea*, *Swartzia*) (figs. 50 and 51), Piperaceae (*Piper*), Rubiaceae (*Genipa*, *Palicourea*), Sapindaceae (*Matayba*), Sapotaceae (*Achras*), Sterculiaceae (*Theobroma*), and Verbenaceae (*Vitex orinocensis*) (August 1981; Fleming 1981; Fleming and Heithaus 1981; Flores 1992a, 1994b, 1994d, 1994e, 1999; Foster 1978, 1990; Gentry 1993; Gottsberger 1983; Janzen 1971a, 1971b; Janzen and others 1976; Levey and others 1994; Morrison 1978; Timm and others 1989; Van der Pijl 1957, 1972; Van Roosmalen 1985).

Primates

As recent colonizers, primates are fundamentally predators that eat all the fruits available but disperse few diaspores. Monkeys prefer fruits with hard pericarp bearing arillate seeds (Van der Pijl 1972). Commonly they eat numerous fruits of the

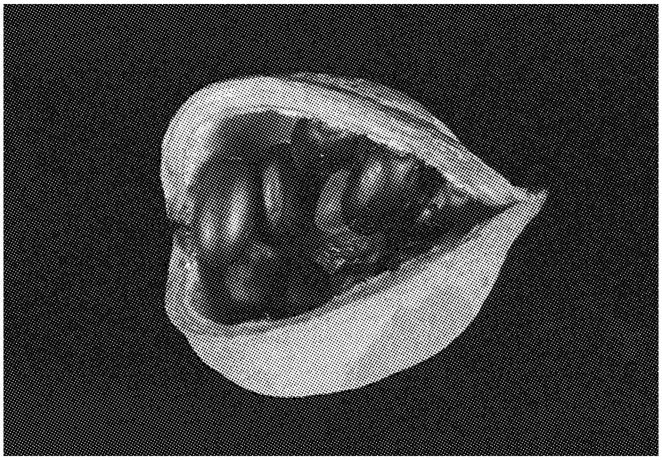

Fig. 107.

following families: Annonaceae (*Annona*, *Guatteria*, *Rollinia*), Anacardiaceae (*Spondias*), Apocynaceae (*Stemmadenia*), Araliaceae (*Dendropanax*), Boraginaceae (*Cordia bicolor*), Burseraceae (*Bursera simaruba*, *Tetragastris*, *Trattinickia*), Fabaceae-Caesalpinioideae (*Cassia grandis*, *Hymenaea courbaril*, *Prioria)* (fig. 50), Capparidaceae (*Capparis*), Caryocaraceae (*Caryocar*), Cecropiaceae (*Cecropia*, *Pourouma*), Chrysobalanaceae (*Couepia*, *Hirtella*, *Licania*, *Parinari*), Clusiaceae (*Garcinia*, *Vismia*), Euphorbiaceae (*Euphorbia*), Flacourtiaceae (*Casearia*, *Zuelania*), Lauraceae (*Ocotea*, *Nectandra*, *Persea*), Lecythidaceae (*Bertholletia*, *Gustavia*, *Lecythis*, *Eschweilera*) (figs. 54 and 106), Melastomataceae (*Miconia*, *Mouriri*), Meliaceae (*Guarea*, *Trichilia*) (fig. 56), Fabaceae-Mimosoideae (*Enterolobium*, *Inga*) (fig.76), Monimiaceae (*Mollinedia*, *Siparuna*), Moraceae (*Brosimum*, *Ficus*, *Helicostylis*, *Maquira*, *Perebea*), Myristicaceae (*Compsoneura*, *Irianthera*, *Virola*, *Otoba*) (fig. 62), Myrsinaceae (*Ardisia*), Myrtaceae (*Eugenia*, *Marliera*, *Myrcia*, *Psidium*, *Syzygium*) (fig. 68), Nyctaginaceae (*Neea*), Olacaceae (*Minquartia guianensis*) (fig.71), Opiliaceae (*Agonandra*), Fabaceae-Papilionoideae (*Dipteryx*, *Swartzia*) (figs. 51-52), Polygonaceae (*Coccoloba*), Quiinaceae (*Lacunaria*), Rhamnaceae (*Ziziphus cinnamomum*, *Z. chloroxylon*), Rubiaceae (*Alibertia*, *Coussarea*, *Faramea*, *Genipa*, *Gonzalagunia*, *Guettarda*, *Palicourea*, *Psychotria*, *Simira*), Rutaceae (*Citrus*), Sapindaceae (*Cupania*) (fig. 59), Sapotaceae (*Chrysophyllum*, *Manilkara*, *Pouteria*), Simaroubaceae (*Picramnia*, *Simarouba amara*), Sterculiaceae (*Guazuma ulmifolia*, *Sterculia*, *Theobroma*) (fig. 107), Tiliaceae (*Apeiba*, *Muntingia calabura*) (fig. 43), Ulmaceae (*Trema micrantha*), and Verbenaceae (*Citharexylum*, *Vitex stahelii*) (Chapman 1989; Croat 1978; Eisenberg 1983; Estrada and others 1984; Flores 1992a, 1992b, 1994d, 1994e, 1999; Gentry 1993; Hladik and Hladik 1969; Howe 1980, 1982; Levey and others 1994; Milton 1980; Van der Pijl 1972; Van Roosmalen 1985; Yumoto and others 1995; Zhang and Wang 1995). Gorillas (*Gorilla gorilla*), chimpanzees (*Pan troglodytes*), and mandrills (*Papio anubis*) also eat several of these fruits (Yamagiwa and others 1993, Yumoto and others 1995).

Humans are active seed dispersers. They gather fruits and use seeds to obtain food, fibers, essential oils, insecticides, beverages, alkaloids, drugs, phytoestrogens, animal fodder, and other products. Seeds are also used to start plantations (see Ethnobotany Chapter).

Other Mammals

Rodents are frequently predators but may behave as commensals and dispersers (dyszoochory). Some eat the diaspore pulp while rejecting the remaining tissues and the seed; some swallow the diaspore and defecate the seeds at other sites; some bury the diaspores to feed on later. However, mammal-diaspore relationships are very complex (Janzen 1983a, 1983c, 1983d, 1983f; Janzen and Wilson 1983). *Microsciurus*, *Sciurus*, *Orthogeomys*, *Heteromys*, *Liomys*, *Proechimys*, *Hesperomys*, *Thmasomys*, *Agouti*, *Dasyprocta*, and *Myoprocta* are active rodents in Neotropical forests; they forage, destroy, bury, and store several diaspores (Fleming 1983a, 1983b; Gottsberger 1983; Paschoal and Galetti 1995; Timm and others 1989). *Sciurus* forages first on the ground and only later climbs the tree to gather additional fruits (Bonaccorso and others 1980, Heaney 1983). The mammals that climb the trees and those that feed on the discarded diaspores attract *Agouti*, *Dasyprocta*, and *Proechimys*. Rodents usually eat the mesocarp and frequently the seed or a part of it. Some seeds with woody endocarps, intact or partially damaged, are transported to different areas or are swallowed and defecated at other sites. Some seeds remain viable and eventually germinate. *Myoprocta exilis* and *Dasyprocta leporina*, dispersal vectors of *Vouacapoua americana* seeds, bury many seeds. These seeds produce seedlings with a higher capacity to survive than those that germinate on the forest floor under the tree crown, where they perish from weevil and termite attacks (Forget 1997).

Among the marsupials, *Philander opossum*, *Didelphis marsupialis*, and *Caluromys derbianus* are active dispersers of fruits and seeds; *Didelphis marsupialis* is the most efficient disperser (Medellín 1994, Timm and others 1989). Some of the diaspores dispersed are those of *Piper*, *Cecropia*, *Dipteryx*, and *Virola.*

All carnivores, except *Lutra* and *Felis*, are frugivorous (Janzen 1983a) and all are potential dispersers of adhesive diaspores (epizoochory) (Gottsberger 1983). *Nasua narica*, *Potos flavus*, and *Eira barbara* are sporadic dispersers of diaspores (Brosset and Erard 1986, Janzen 1983c, Jordano 1983, Kaufmann 1983). *Chrysocyon* and *Cerdocyon*, species from the fauna of the Brazilian cerrado, feed on seeds and fruits (Gottsberger 1983, Vieira and Carvalho-Okano 1996). The tapirs (*Tapirus bardii*, Perissodactyla) bury part of the seeds, promoting the creation of new seedling populations (Janzen 1983f).

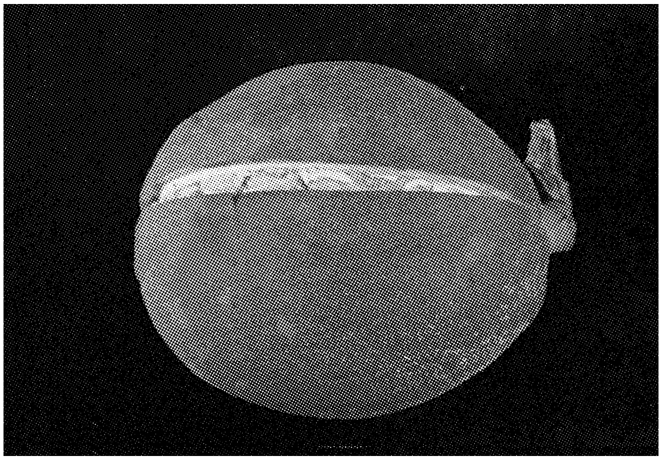

Fig. 108.

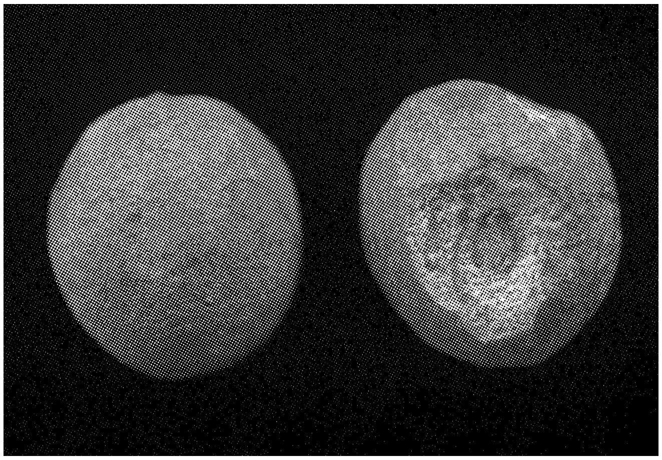

Fig. 109.

Fig. 110.

Tayassu tajacu (Artiodactyla) eat, bury, and defecate seeds thus contributing to seed dispersal (Kiltie 1981, Sowls 1983). *Odocoileus virginianus* (Artiodactyla, Cervidae) eat diaspores of several species but do not swallow the seeds; they are ejected when the soft tissues are chewed (Janzen 1983d). All mammals consume diaspores with attractive color, and scarce pulp, but with tissues very rich in lipid content such as the fruit mesocarp or the sarcotesta, embryo, and endosperm from the seed. They also eat hard, indehiscent, nonedible fruits with no attractive color. These fruits contain from one to several seeds rich in lipids (Van Roosmalen 1985).

Elephants are efficient dispersers of diaspores (Alexandre 1978, Gautier-Hion and others 1985, White and others 1993, Yumoto and others 1995). They prefer fruits with dry, fibrous pericarp and well-protected seeds. These fruits are dull brown, yellow-brown, blackish-brown, light brown, yellow-orange, or green (Gautier-Hion 1990, Gautier-Hion and others 1985). Examples of diaspores dispersed by elephants include *Antrocaryon nannanii* (Anacardiaceae), *Anonidium mannii* (Annonaceae), *Mammea africana* (Clusiaceae), *Uapaca guineensis* (Euphorbiaceae), *Tetrapleura tetraptera* (Fabaceae-Mimosoideae), *Treculia africana* (Moraceae), *Omphalocarpum* (Sapotaceae), *Klainedoxa gabonensis* (Simaroubaceae), *Grewia milbraedii* (Tiliaceae), and *Cissus dinklagei* (Vitaceae) (Yumoto and others 1995).

The following are fruits and seeds commonly consumed and dispersed by mammals: Anacardiaceae (*Spondias*), Annonaceae (*Duguetia*), Bombacaceae (*Pachira*) (fig. 108), Boraginaceae (*Cordia*), Burseraceae (*Protium*), Caryocaraceae (*Anthodiscus*, *Caryocar*), Chrysobalanaceae (*Couepia*, *Licania*, *Parinari*), Combretaceae (*Terminalia cattapa* L.), Euphorbiaceae (*Croton floribundus*, *Dalechampia pentaphylla*), Fabaceae-Caesalpinioideae (*Cynometra*, *Hymenaea*), Fabaceae-Papilionoideae (*Andira*, *Dipteryx*) (figs. 51 and 52), Fagaceae (*Quercus*), Humiriaceae (*Humiriastrum*, *Sacoglottis*, *Vantanea*) (fig. 109), Juglandaceae (*Alfaroa*, *Juglans*) (fig. 110), Lauraceae (*Ocotea*), Lecythidaceae (*Bertholletia*, *Couroupita*, *Eschweilera*, *Gustavia*, *Lecythis*) (figs. 54 and 106), Malpighiaceae (*Byrsonima crassifolia*, *Dicella bracteosa*), Meliaceae (*Cabralea canjereana*, *Carapa*, *Guarea grandifolia* DC.) (fig. 56), Fabaceae-

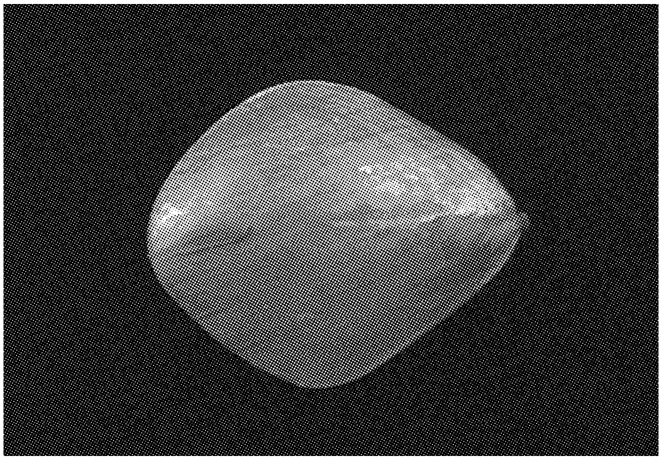

Fig. 111.

Mimosoideae (*Enterolobium*, *Pentaclethra macroloba*, *Stryphnodendron*) (fig. 111), Moraceae (*Brosimum*, *Ficus*), Myrsinaceae (*Ardisia*), Myrtaceae (*Eugenia ligustrina*), Polygalaceae (*Diclidanthera laurifolia*), Rubiaceae (*Alibertia*), Sapotaceae (*Achras*, *Chrysophyllum cainito*, *Manilkara*), Sterculiaceae (*Guazuma ulmifolia*, *Luehea*, *Sterculia*) (figs. 108 and 112), Ulmaceae (*Celtis iguanae*), and Verbenaceae (*Citharexylum*, *Vitex*) (Fleming 1983a, 1983b; Gentry 1993; Janzen 1983a, 1983c, 1983d, 1983f; Kaufmann 1983; Paschoal and Galetti 1995; Van Roosmalen 1985).

Myrmecochory

Ants do not play an important role in the dispersal of diaspores (Van der Pijl 1972). Ant-dispersed fruits are small, and dehiscent with seeds having an elaiosome rich in lipids; usually these seeds are too small to attract birds (Thompson 1981, Van der Pijl 1972, Van Roosmalen 1985). Some species move the seeds 1 to 2.5 m. Frequently, ants deposit seeds in their nests, and many of these germinate and develop into healthy seedlings (Passos and Ferreira 1996).

Saurochory

Several reptiles are frequent diaspore dispersers in the Tropics. The turtle *Rhinoclemmys annulata*, the lizard *Basiliscus basiliscus*, and the iguana *Iguana iguana* eat and transport fruits and seeds of species such as *Spondias* (Anacardiaceae), *Cordia* (Boraginaceae), *Sloanea* (Elaeocarpaceae) (fig. 103), *Macrolobium*, *Swartzia* (Fabaceae-Caesalpinioideae), *Inga* (Fabaceae-Mimosoideae) (fig. 76), *Ficus*, *Brosimum* (Moraceae), and *Ardisia* (Myrsinaceae) (Berg 1975, Ernst 1983, Gottsberger 1978, Rand 1978, Van Devender 1983).

Ichthyochory

The proportion of diaspores dispersed by fish in the riparian and inundated forests is high, although it has not been precisely quantified (Gottsberger 1978, Goulding 1980, Howe and Smallwood 1982). Fish dispersed 16 forest tree species and destroyed 17 species in the varzea forests (riparian plains, rivers with clear waters) of the Brazilian Amazon. Gottsberger (1978) proposed that ichthyochory is an archaic method of dispersal and that the incidence is high in waters poor in nutrients, a finding that suggests fish depend on nutritious fruits and seeds.

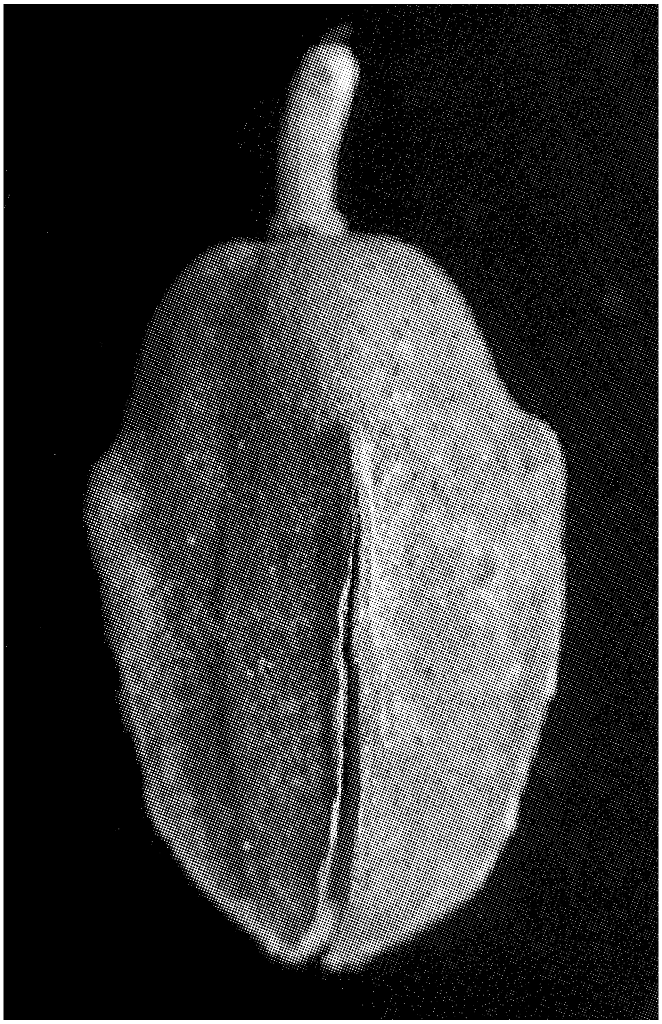

Fig. 112.

In the varzea and the igapó (riparian plains and rivers with dark waters), peak fructification coincides with the period of flooding. In the inundated forests almost all diaspores fall into the water where they are eaten by fish, with variable rates of destruction. Ichthyochory can be facultative or obligatory (Kubitzki and Ziburski 1994).

Ichthyochoric diaspores can have ariloid structures (*Annona*, *Virola*). Some have protective structures such as a hard pericarp (*Cecropia*), woody endocarp (*Licania*, *Astrocaryum*), hard seedcoat (some Elaeocarpaceae, *Unonopsis*), sarcotesta, and fleshy tissues with agreeable taste or attractive infrutescence (Gottsberger 1978) (fig. 62). Many of the diaspores dispersed by fish or water and fish have structural adap-

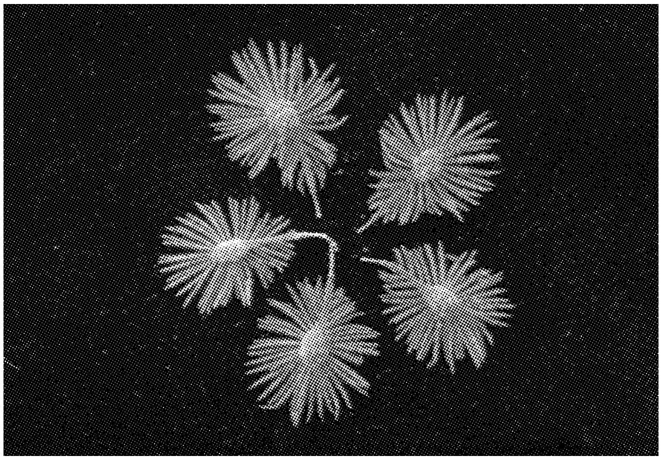
Fig. 113.

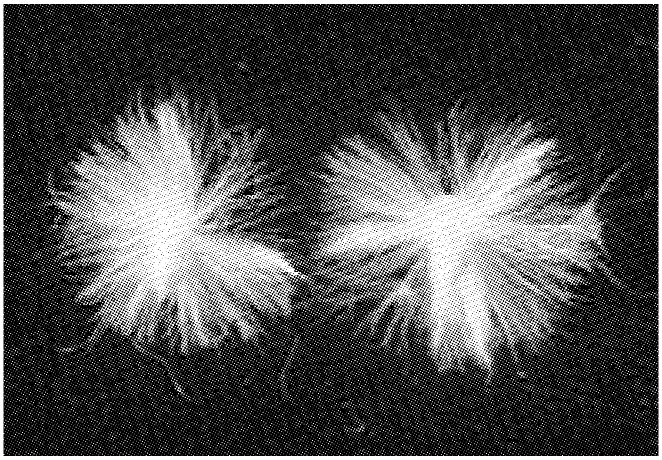
Fig. 114.

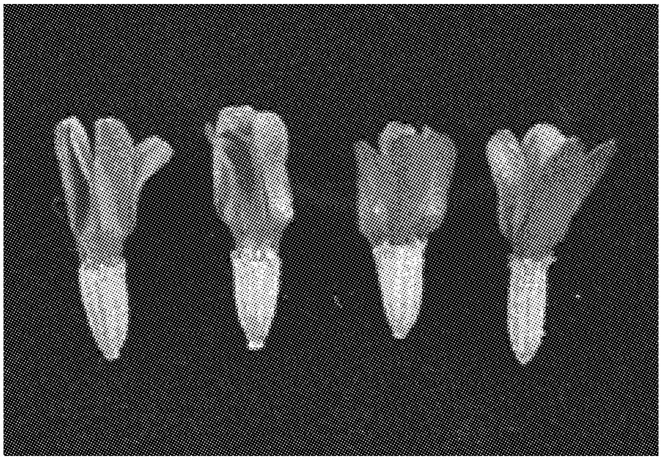
Fig. 115.

tations for staying afloat for long periods in inundated forests. Finally, they sink and germinate near the end of the immersion period (Kubitzki and Ziburski 1994).

Neotropical rivers contain many species of disperser fish: *Cichlasoma* (Cichlidae), *Brycon* (Characidae, highly predatory), *Rhamdia* (Pimelodidae), *Colossoma* (Characidae), *Cytocharax* (Characidae), *Leporinus* (Curimatidae), *Lithodoras dorsalis* (Doradidae); they feed on the diaspores that fall into the water (Flores 1992c, 1999; Gottsberger 1978). These fish contribute to dispersal of seeds of the following trees: *Anacardium* (Anacardiaceae); *Annona hypoglauca, Annona, Duguetia, Unonopsis* (Annonaceae); *Crescentia amazonica, Tabebuia barbata, T. palustris* (Bignoniaceae); *Pseudobombax* (Bombacaceae); *Protium* (Burseraceae) (figs. 72 through 73); *Crataeva benthamii* (Capparidaceae); *Cecropia membranacea, C. latiloba* (Cecropiaceae); *Buchenavia oxycarpa* (Combretaceae); *Sloanea* (Elaeocarpaceae) (fig. 103); *Hevea spruceana* (Euphorbiaceae); *Aldina latifolia, Crudia amazonica, Cynometra, Macrolobium, Mora oleifera, M. paraensis* (Fabaceae-Caesalpiniodeae); *Swartzia* (Fabaceae-Papilionoideae); *Laetia corymbulosa, L. suaveolens* (Flacourtiaceae); *Aniba, Licania, Nectandra, Ocotea* (Lauraceae) (fig. 70); *Eschweilera ovalifolia, E. tenuifolia, Lecythis* spp. (Lecythidaceae) (figs. 54 and 106); *Byrsonima* (Malpighiaceae); *Carapa guianensis, Guarea, Trichilia* (Meliaceae) (fig. 56); *Brosimum, Ficus* (Moraceae); *Virola, Otoba* (*Myristicaceae*) (fig. 62); *Genipa, Randia* (Rubiaceae); and *Vitex cymosa* and *V. cooperi* (Verbenaceae) (Flores 1992c, 1999; Gottsberger 1978; Kubitzki and Ziburski 1994).

Sometimes fish drop the seeds and the streams transport them long distances; eventually the seeds reach a riverbank where they sometimes germinate (Flores 1992c, 1999). In the Brazilian Amazon, fish play an important role as dispersers (Gottsberger 1978, Goulding 1980). Preliminary information on the role of fish in the Atlantic lowlands of Mesoamerica leads one to similar conclusions.

Abiotic or Azoochorous Dispersal

The three types of abiotic dispersal are discussed in the following sections.

Anemochory

Tropical trees produce a great variety of wind-dispersed diaspores (Van der Pijl 1972). Light fruits can have a winged pericarp (*Terminalia amazonia*, Combretaceae; *Hymenolobium, Sclerolobium*) (fig. 45) or filiform projections (*Heliocarpus appendiculatus*, Tiliaceae) (fig. 113). Some seeds have a winged seedcoat (*Tabebuia rosea*, Bignoniaceae; *Cedrela odorata, Vochysia guatemalensis*) (figs. 91-93); other seeds are pubescent and lanate (*Bombacopsis quinata*, Bombacaceae; *Macrohasseltia macroterantha*, Flacourtiaceae) (fig. 114). Some units of dispersal (fruit + modified floral organs such as androecium, perianth, and receptacle) have additional floral parts to aid in dispersal. Examples include *Oreomunnea pterocarpa* (Juglandaceae) (fig. 115) with a nut surrounded by a modified perianth; *Triplaris americana* and *Coccoloba tuerckheimii* (Polygo-

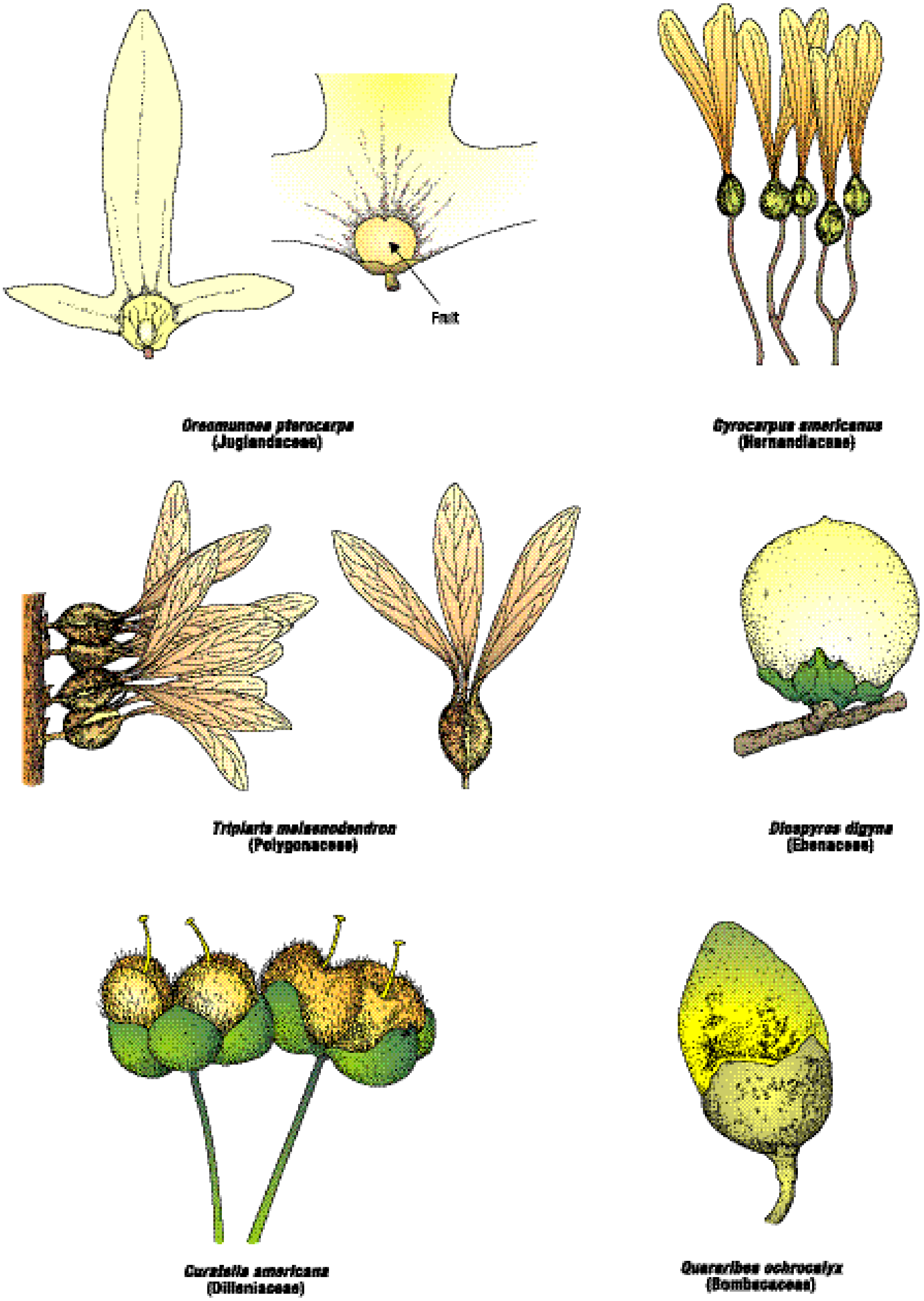

Fig. 116. Different types of diaspores.

Fig. 117.

Fig. 118.

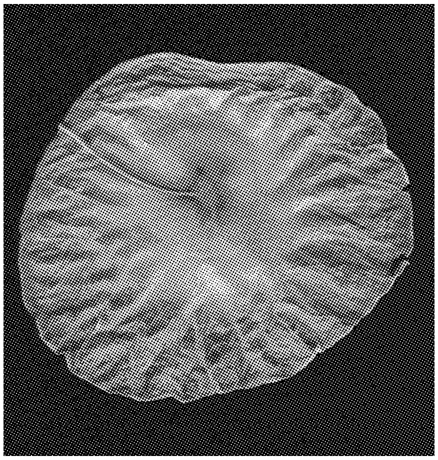

Fig. 119.

naceae) with a nut enclosed in an acrescent perianth that extends after fertilization; *Gyrocarpus jatrophifolius* and *Hernandia didymantha* (Hernandiaceae) with a nut immersed in a cup formed by perianth tissues; *Astronium graveolens* (Anacardiaceae) with a drupe surrounded by a winged calyx growing in the postfertilization stages and masking the petals; and *Curatella americana* (Dilleniaceae) (fig. 116), *Diospyros nicaraguensis* (Ebenaceae), and *Cordia alliodora* (Boraginaceae) (fig. 116), with a conspicuous calyx, acrescent and persistent.

The morphological design of wind-dispersed diaspores seems to slow their descent and increase their exposure to horizontal or gusty winds (Augspurger 1986, Rabinowitz and Rapp 1981). The rate of descent is correlated with the wing loading (weight/area) of the diaspore (Green 1980). Horizontal winds disperse the diaspores over a wide area, with potential dispersal and area inverse to the descent rate (Augspurger 1986). The consistency in direction, intensity, and speed of the wind also affects the seed shadow.

Using the morphology of the diaspore, the rotatory movement, and the rate of descent, Green (1980) established two categories of wind-dispersed diaspores: rolling samaras, which autorotate around the longitudinal axis of the diaspore and autogyrate around one end of the diaspore, and autogyros, or nonrolling samaras, including the samaras that only autogyrate. For a determined wing loading the first have a higher descent rate (Augsburger 1986, Green 1980, Norberg 1972). The morphology and the aerodynamic behavior led Augsburger (1986) to group the wind-dispersed diaspores studied into six types:

(1) The floater is a diaspore that floats downward in a vertical line; e.g., *Bombax*, *Bombacopsis*, *Ceiba*, *Ochroma*, *Pseudobombax* (Bombacaceae), *Trichospermum* (Tiliaceae).

(2) The rolling autogyro is a diaspore that rotates on two axes: around the longitudinal axis of the diaspore and around one end of the diaspore in a closed spiral (rolling samara, per Green 1980); e.g. *Cespedesia* (Ochnaceae); *Couratari* (Lecythidaceae); Dalbergia, *Hymenolobium*, *Lonchocarpus*, *Machaerium*, *Platymiscium* (Fabaceae-Papilionoideae); *Lafoensia punicifolia* (Lythraceae); *Sclerolobium*, *Tachigali* (Fabaceae-Caesalpinioideae); *Terminalia amazonia*, *T. oblonga*, *T. bucidoides* (Combretaceae); and *Vochysia*, *Qualea* (Vochysiaceae) (figs. 45-46, 91, 117-118).

(3) The autogyro is a diaspore that rotates closely around the diaspore end containing the seed; e.g. *Loxopterygium sagotii* (Anacardiaceae); *Cedrela*, *Swietenia* (Meliaceae); *Luehea* (Tiliaceae); *Myroxylon*, *Vatairea* (Fabaceae-Papilionoideae) (figs. 92 and 112).

(4) The undulator is a diaspore that glides and undulates but not with accumulative forward motion; its gliding is discontinuous or it oscillates fugaciously (nonrolling samara, per Green 1980); e.g. *Aspidosperma* (Apocynaceae), *Pterocarpus* (Fabaceae-Papilionoideae), and *Jacaranda* (Bignoniaceae) (figs. 47 and 119).

(5) The helicopter is a diaspore that spins tightly around a vertical line; it is similar to the autogyro with additional wings; e.g. *Astronium graveolens* (Anacardiaceae), *Cordia alliodora* (Boraginaceae), *Triplaris* (Polygonaceae), and *Macrohasseltia* (Flacourtiaceae) (figs. 114-116).

(6) The tumbler is a diaspore that tumbles with an inconsistent axis, at random. It can also rotate around a vertical line in an open and extended spiral; e.g. *Cavanillesia* (Bombacaceae).

The unclassified diaspores include those with variable behavior; e.g., *Tabebuia* (Bignoniaceae) (fig. 93).

Fig. 120.

Hydrochory

Hydrochory is carried out by rain-wash (*ombrohydrochory*), rivers, or marine streams (*nautohydrochory*). It plays an important role in the dispersal of riparian, marshy, or coastal tree diaspores (Kubitzki and Ziburski 1994, Van der Pijl 1972). In some cases the diaspores float; in others, they submerge. The seeds of *Astrocaryum*, *Cocos nucifera* (Arecaceae), *Tabebuia palustris* (Bignoniaceae), *Calophyllum brasiliense* (Clusiaceae), *Hevea brasiliensis* (Euphorbiaceae), *Aldina latifolia*, *Crudia amazonica*, *Cynometra*, *Eperua*, *Macrolobium*, *Mora oleifera*, *M. paraensis* (Fabaceae-Caesalpinioideae), *Parkia discolor* (Fabaceae-Mimosoideae), *Pterocarpus*, *Swartzia* (Fabaceae-Papilionoideae), *Bertholletia excelsa*, *Eschweilera* spp., *Grias cauliflora*, *Gustavia superba* (Lecythidaceae), *Carapa guianensis* (Meliaceae), and *Calatola costaricensis* (Icacinaceae) can be dispersed by river or rivulet streams or by inundation of riparian plains (figs. 105 and 120). To increase their floating capacity, the seeds are dispersed primarily by hydrochory, which reduces the specific gravity, increases the surface area, and deposits a thick cuticle on the outer surface. The existence of aerenchyma is a common device.

Autochory

Several taxa use autochoric dispersal. The fruit wall commonly dictates use of this mechanism. The explosive release of seeds is an ancient characteristic (Van der Pijl 1972). Autochory is frequent in arid zones (Van der Pijl 1972), but it is also observed in tropical forest trees, e.g., some Fabaceae.

Active Ballistics

The active ballistics of diaspores occurs when tension increases in hygroscopic, dead tissues. Tension in dead tissues is present in *Croton priscus, Hevea brasiliensis,* and *Hura crepitans* (Euphorbiaceae); some species of *Cassia* and *Crudia* (Fabaceae-Caesalpinioideae); and several species of *Calliandra*, *Mimosa*, and *Pentaclethra macroloba* (Fabaceae-Mimosoideae) (figs. 65-66).

Passive Ballistics

This occurs when an external agent (wind, rain, or animal) releases the inner tension of the fruit and provides the necessary energy for the opening of the fruit. The mechanism is common in herbaceous species (Van der Pijl 1972).

Creeping Diaspores

In creeping diaspores the movement of the adhesive structures is provoked by weather changes (moistness-dryness). It is common in Asteraceae and Poaceae (Van der Pijl 1972).

Barochory

This is dispersal by weight (Van der Pijl 1972); e.g., *Billia hippocastanum*, *B. columbiana* (Hippocastanaceae), *Quercus* (Fagaceae), *Rhizophora* (Rhizophoraceae), *Juglans* (Juglandaceae), *Carapa*, *Guarea* (Meliaceae), *Mora* (Fabaceae-Caesalpinioideae), *Dipteryx* (Fabaceae-Papilionoideae), *Achras*, *Manilkara* (Sapotaceae) (figs. 42, 52, and 56).

GERMINATION

Germination is, in a nutshell, the process unchained by seed hydration (imbibition) and the beginning of radicle expansion (Evenari and others 1957). Embryogeny and germination are, then, successive stages in the development of the new sporophyte, separated by a period of relative metabolic inactivity called quiescence (Bewley and Black 1978, 1982, 1994; Flores 1999).

The process of germination involves the transition of cells from a dehydrating stage and low metabolic activity to a hydrated and metabolically active stage. Water is absorbed by many seeds in a triphasic way: imbibition, germination sensu stricto, and embryo development (Bewley and Black 1994, Tissaoui and Côme 1975). Imbibition corresponds to the rapid absorption of water leading to a regular increment in the respiratory activity. Germination sensu stricto is the process of embryo activation, not accompanied by any apparent morphological change. Embryo development is marked by the initiation of radicle elongation and a significant change in the physiology of the embryo (Côme and Corbineau 1996a, 1996b). The crucial phase is the germination sensu stricto, because seedling development depends on it. In most cases, the seed germinates only if the respiration and production of adenosine 5'-triphosphate (ATP) are adequate, creating an oxygen requirement (Côme and Corbineau 1996a, 1996b).

Germination culminates with radicle development (basically cellular elongation) and its protrusion into the adjacent tissues. In recalcitrant seeds with minute, rudimentary embryos or large embryos with a rudimentary radicle (reduced to a radical meristem), the development of the radicle implies cell division and elongation.

ENVIRONMENTAL INFLUENCES

The external environmental factors regulating the activity of the maternal tree during seed maturation include temperature, light, photo- and thermoperiod, relative air moisture, and water potential in the soil. The internal parameters, that is, the water potential of the maternal tree and its nutritional and hormonal state, and the position of the seed on the tree also affect seed maturation. Other environmental factors involved directly in the process of germination are temperature, light, and gas (Bewley and Black 1994, Bonner 1966).

Water

In seeds undergoing maturation drying, water imbibition is the first requirement for germination because it permits metabolic reactivation and restoration of the entire system of membranes and organelles. Activation of the enzymatic system, respiration, and synthesis of RNA and proteins are fundamental. The enzymes participating in the process are found in the dehydrated seed or are synthesized during imbibition. In most cases, the water imbibing the seed is equivalent to two or three times the dry weight of the seed. The net diffusion occurs in a descendent gradient of water potential (or energetic state of the water i); in other words, from pure water to water containing solutes (Bewley and Black 1994). The potential of a cell inside a seed is determined by the osmotic potential (c_p), determined by the concentration of solutes (more solutes = less osmotic potential), the matric component (c_c), determined by the hydration of matrices (cell walls, starch, protein bodies), and the pressure potential (c_p), permitting water intake and putting pressure on the cell wall (Bewley and Black 1994, Leopold and Kriedemann 1975). In the water potential of the soil, only c_c has an important function. Water absorption has three phases:

(1) A rapid phase of initial imbibition that is strongly influenced by the matric forces. This phase occurs in both viable and nonviable seeds, because the water potential of the mature seed is lower than that of the surrounding humid soil. In this phase, energy is liberated as heat; the gases of colloidal adsorption and the solutes are released as sugars, organic acids, ions, amino acids, and proteins. The solutes may stimulate the growth of bacteria and the fungi of the soil. An imbibitional pressure is also created through protein hydration (colloid formation) (Bewley and Black 1994, Bonner and others 1994).

(2) A phase of slow water intake, in which the matric component (c_c) is not important and the water potential of the seed (c) is determined by $c_{\check{s}}$ and c_p. This is the phase when metabolic activity begins. Dormant seeds are also metabolically active; the length of this phase is correlated with the intensity of the dormancy (Bewley and Black 1994, Bonner and others 1994).

(3) The last phase occurs only in nondormant seeds involved in active germination. It is a rapid phase intensified by metabolism activation; in many cases, it coincides with the breaking of the seedcoat and the beginning of the elongation and protrusion of the radicle (Bewley and Black 1994, Bonner and others 1994). In orthodox seeds, the endosperm and the cotyledons do not expand if the seedlings are cryptocotylar. In recalcitrant seeds with rudimentary embryos, cotyledon development frequently precedes radicle development (e.g., *Virola*) or both develop concurrently (e.g., *Minquartia guianensis*). Seeds with nuclear endosperm may finish cell wall deposition in this stage, and endosperm disintegration either in the middle or around the embryo occurs (fig. 81).

Reserve mobilization and enzymatic activation depend on hydration; the best germination occurs with a low moisture tension (0.005 to 0.500 bars). If the tension is zero, the water pellicle around the seed inhibits the absorption of oxygen (Bonner and others 1994, Mayer and Shain 1974). During reserve mobilization, the insoluble forms are transformed into soluble forms. The amylases are the first enzymatic system involved in the transformation of starch into soluble sugars. The lipases enfold the lipids in fatty acids and glycerol. The fatty acids are b-oxidated to acetyl-coenzyme A, which enters the glyoxylate cycle and eventually forms carbohydrates. Some proteins are important as sources of nutrients and are converted to soluble forms. The movement of substances inside the embryo is vital. In many species the stimulus controlling the amylase activity arises in the radicle; other stimuli arise in the cotyledons (Bewley and Black 1994, Bonner and others 1994, Leopold and Kriedemann 1975, Mayer and Shain 1974, Stanwood and McDonald 1989).

Temperature

The effect of temperature is difficult to separate from the effects of light and water. Under natural conditions, temperature determines the capacity and rate of germination, removing the primary and inducing secondary dormancy (Bewley

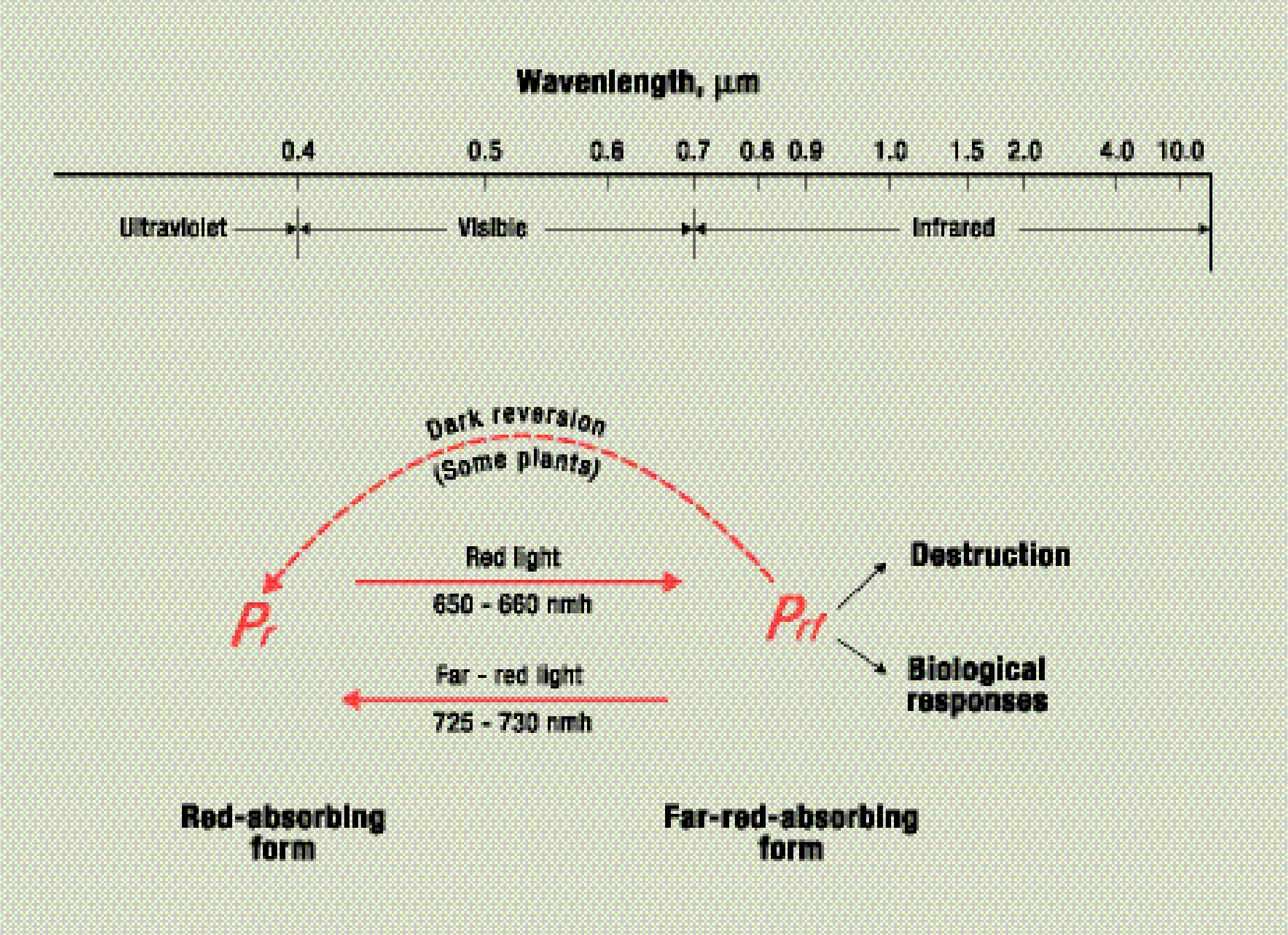

Fig. 121. Light spectral composition and exposure of phytochrome to red light and conversion to the far-red-absorbing form and viceverse.

and Black 1994, Bonner and others 1994, Leopold and Kriedemann 1975, Mayer and Shain 1974, Stanwood and McDonald 1989). For germination, the upper limit is about 45 °C and the lower 3 to 5 °C. Many species germinate at about 40 °C, but the seedlings are abnormal; others can germinate near the lower temperature limit but they rarely produce normal seedlings (Bonner and others 1994). The regimes of alternating temperature (20 °C at night and 30 °C during the day) seem optimal for species from temperate zones, although similar results are obtained with constant temperatures of 25 °C (Bonner and others 1994). In tropical species the best range is usually 25 to 30 °C.

Light

Light stimulates germination, but it is not strictly necessary for most seeds; however, some pioneer tropical species typical of areas in early succession, such as *Cecropia* and *Heliocarpus,* have photoblastic seeds. A pigment called phytochrome is involved in the photocontrol of the germination; it exists in two reversible forms. The *Pr* form (red light) has a maximal absorbency of 660 nmh and stimulates germination; the *Pfr* form (far-red light) has a maximal absorbency of 730 nmh and inhibits germination (fig. 121) (Bonner 1966, Hendricks and Borthwick 1967, Hillman 1969). The far-red light can reverse the effects of the red light. If seeds are exposed to red and far-red light consecutively, failure to germinate depends on which light was used. Exposure to red light for less than a second can produce the stimulus to unchain germination; this effect is magnified if infrared light is applied later. When the treatment is reversed, the seed does not germinate (Bonner 1966, Kozlowski 1971, Leopold and Kriedemann 1975).

When the *Pr* is illuminated with red light, it changes to *Pfr*; if the latter absorbs far-red light it converts to *Pr* (fig. 121). Inside the seed, the *Pfr* is converted metabolically to *Pr* even in darkness. The *Pfr* can also be metabolically destroyed and the *Pr* resynthesized (Bonner 1966, Kozlowski 1971, Leopold and Kriedemann 1975).

Light sensitivity is influenced by pretreatment with temperature. With an increment of cold pretreatment, seed germination can be increased in darkness and the sensitivity to far-red light decreased. The requirement of light for germination varies with the amount of imbibed water (Bonner and others 1994, Kozlowski 1971).

GENETIC INFLUENCE

A factor always neglected and one that has not been well evaluated is how the genome received by the diaspore controls germination. Several parts of the diaspore differ in genotype; the tissues of the fruit, other tissues surrounding the seed, and the seedcoat have the maternal genotype. The endosperm is one-third paternal and two-thirds maternal in the most common type of seed. The embryo is one-half paternal and one-half maternal. In general, the genotype of one or both parents affects the structure and composition of the various parts of the diaspore. For example, the genes expressed in the megagametophyte play a role in the induction of seed development, primarily in embryo and endosperm development (Angenent and Colombo 1996, Ray 1998). The endogenous annual rhythm of the germinability of the seed and the internal mechanisms regulating it are not well known either.

SEED RESPIRATION

Respiration permits the acquisition of energy. It requires oxygen and the removal of CO_2. High levels of CO_2 can inhibit germination, and a lack of oxygen has the same effect although some species can germinate in anaerobic conditions (Bewley and Black 1994, Bonner and others 1994, Leopold and Kriedemann 1975).

The inhibited seed has three active routes of respiration: glycolysis, pentose-phosphate, and the citric acid cycle (Krebs cycle). Glycolysis–catalyzed by cytoplasmic enzymes–and the Krebs cycle (inside the mitochondria) are essential for the production of ATP. The Krebs cycle produces ATP through the cyclic metabolism of organic acids. The pentose phosphate route is a source of reduced nicotine adenine dinucleotide phosphate (NADPH); it acts as a hydrogen and electron donor in reductive biosynthesis, especially of fatty acids. Intermediate compounds, which initiate other biosynthetic processes producing energy, also exist in this route (Bewley and Black 1994, Leopold and Kriedemann 1975).

According to Bewley and Black (1994), the respiratory process in the orthodox seed involves three or four stages:

(1) High oxygen (O_2) consumption and a linear increment in respiration during tissue hydration (hydration and activation of mitochondrial enzymes in the Krebs cycle and the electron chain).

(2) Decrease in the respiration proportional to the stabilization of O_2 intake. The seed is hydrated and the enzymatic system is active. Between stages (2) and (3), the radicle protrudes through the surrounding tissues (it coincides with phases (2) and (3) of the imbibition process). The seedcoat (or seedcoat + endocarp or pericarp) can be a physical barrier limiting O_2 intake.

(3) Respiratory reactivation due to activation of the embryo axis and meristems and mobilization of stored reserves. The breaking of the seedcoat may contribute to increasing the intake of O_2.

(4) Respiration restricted to storage tissues whose reserves are being degraded and removed.

The dicotyledon embryo can be complete, large or small, differentiated, partially differentiated, rudimentary, or not differentiated. Cell activation in all embryo tissues appears sequential and in numerous cases it begins in the hypocotyl and extends to the embryonic poles. In the embryo, gradients of activation are at all levels. The sequence of activation in the cotyledons is quite complex and varies with the species (Bewley and Black 1982, 1994). The differentiation of the preexisting cellular organelles and the synthesis of new complementary ones occurs during early germination. The endosperm disintegration takes place in late germination and seems to be regulated by the gibberellins produced in the embryo.

LONGEVITY, VIABILITY, AND DORMANCY

The regeneration of plant communities depends on the seeds reaching a suitable place at the right time. They must have an adequate physiological state to germinate and develop seedlings when the opportunity to regenerate or colonize is available. In some cases, the requirements are satisfied by a strategy of germination in which the seeds germinate as soon as they reach the ground; in other cases, the seeds remain for long periods of time in the ground forming seed banks (pioneers or typical of early succession), with part of the population germinating intermittently. Some seeds live a long time in the soil (Murdoch and Ellis 1992). The period of time in which the seed remains viable in the ground is called longevity. Viability is the germinative capacity; its loss is the final stage of seed deterioration. Seed aging produces a gradual declination of many seed capacities such as germination rate, culminating in seed death (Bewley and Black 1994, Murdoch and Ellis 1992). Species from wet tropical forests tend to lose viability rapidly; perhaps 60 to 70 percent lose it in 3 to 6 months. Some species lose viability in days or weeks (Nichols and González 1991).