

Ecological Distribution of Chlorophyllous Developing Embryos among Perennial Plants in a Tropical Deciduous Forest

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ABSTRACT

A dry-season survey of the developing seeds of 74 species of Costa Rican deciduous forest perennial plants found that the developing embryos of 55 percent of the species were highly chlorophyllous; these species had flat, strap-like or cylindrical fruits with seeds less than 1 g mature weight, or had fully insolated spheroidal fruits with four or less small- to medium-sized seeds. The achlorophyllous seeds were in fruits with large seeds, fruits with many seeds packed in layers, or in fruits borne in locally shady habitats. The presence of a chlorophyllous developing embryo would seem to add significant complexity to the already-complex parasite-host relationship of the embryos that are developing in the fruit, in that fruit and seed-coat traits are evolutionarily affected by transmission of light to the embryo and a photosynthetic embryo may be able to develop more independently of the parent than can an achlorophyllous embryo.

THE DEVELOPING EMBRYOS of many species of plants are deep green due to the presence of chlorophyll and chloroplasts similar to those of leaves (Dahlgren 1980, Yakovlev and Zhukova 1980). In plants with dormant seeds, the chlorophyllous embryos become achlorophyllous upon maturing and remain that way during seed dormancy, suggesting that the chlorophyllous state is of value to the developing embryo, rather than simply being an early stage of seedling development. If this is so, there should be ecological correlates with chlorophyllous seeds. I surveyed the developing seeds and associated fruit traits in 74 species of native perennial shrubs, trees, and lianas in the middle of the dry season in a Costa Rican lowland deciduous forest (Santa Rosa National Park, northwestern Guanacaste Province) and found three such correlates. The species were chosen by virtue of being all those that I could find bearing green fruits during a three-day period (8-10 March 1980).

The embryos (cotyledons plus radicle, hypocotyl, etc.) of 55 percent of the species were intense leaf-green during a long portion of their development. Chlorophyllous embryos were found in all species that bore fully insolated fruits that were flat, strap-like or cylindrical with small- to medium-sized seeds of less than 1 g mature weight, and in almost all highly insolated spheroidal fruits with four or less small- to medium-sized seeds (fig. 1a-e; table 1). An instructive exception was *Lantana camara*, which had fruits that were small, green, single-seeded spheres (2-4 mm diameter) that matured in full sunlight, yet the developing embryos were never green. However, the fruits were arranged in a tight cluster, and therefore the entire infructescence was similar to a single large fruit with many small seeds scattered through it. The embryos of 45 percent of the species

were never chlorophyllous (table 1). These species had very large seeds (e.g., *Dioclea megacarpa* (fig. 1g), *Andira inermis*, *Sapranthus palanga*, *Acrocomia vinifera*), had many seeds packed in several layers in spheroidal or thick cylindrical fruits (e.g., *Apeiba tibourbou* (fig. 1f), *Carica papaya*, *Sapranthus palanga*, *Crescentia alata*, *Tabebuia rosea*, *Brassavola nodosa*), or grew in locally shaded habitats (e.g., *Ardisia revoluta*, *Aphelandra deppeana* (fig. 1h), *Hirtella racemosa*). Additionally, the achlorophyllous embryos of two sapindaceous species had deep-green seed coats and therefore could be said to live in a heavily shaded microhabitat. In all other species surveyed (72), the developing seed coats were translucent white and the developing fruits were leaf-green. The mature and dormant seeds of all 74 of the surveyed species are achlorophyllous. It is clear that chlorophyllous-developing embryos are found in strongly insolated-developing fruits, fruits with all the seeds about equally close to the surface, and fruits and seeds thin or small enough that light penetrates to the embryo. This conclusion constitutes an alternative hypothesis to the view (Dahlgren 1980, Yakovlev and Zhukova 1980) that the presence of chlorophyllous embryos is a family-level trait dependent on taxonomic rather than ecological circumstances.

Studies of photosynthate production and allocation by fruits of trees (Bazzaz *et al.* 1979) and crop herbs (Andrews and Svec 1975, Atkins and Flinn 1978, Atkins *et al.* 1977, Biscoe *et al.* 1975, Crookston *et al.* 1974, Elmore 1973, Enyi 1962, Flinn and Pate 1970, Flinn *et al.* 1977, Harvey *et al.* 1976, Hedley *et al.* 1975, Johnson *et al.* 1975, Kriedemann 1966, Lovell and Lovell 1970, Quebedeaux and Chollet 1975, Sambo 1977, Thorne 1965, Wilmer and Johnston 1976) show clearly that a fruit may contribute

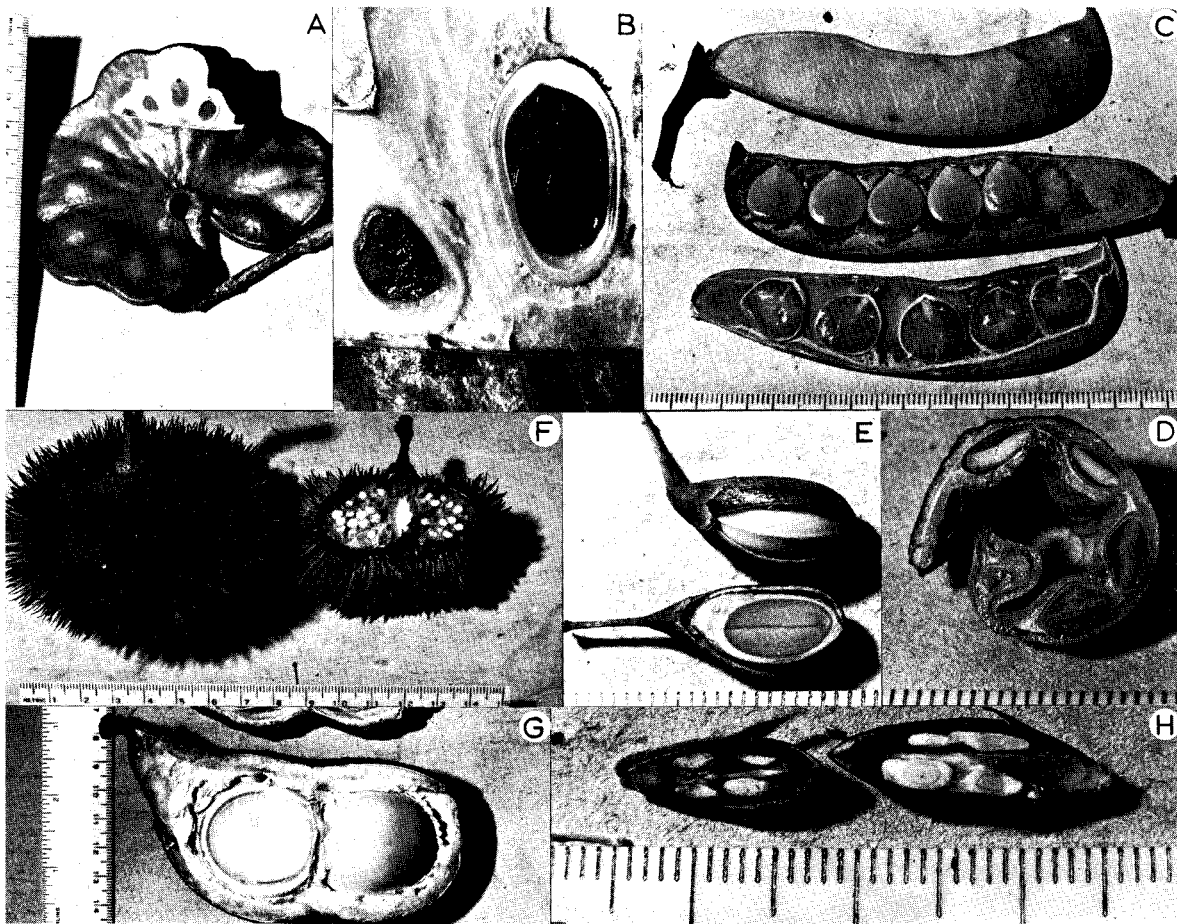


FIGURE 1. A. Full-sized green fruit of *Enterolobium cyclocarpum* with partial section to expose nearly full-sized green embryos. B. close-up of section in (A) showing dark-green embryo (cotyledon) sectioned longitudinally within white, translucent seed coat within white mesophyll next to green pericarp (bottom). C. Intact bright-green, immature, full-sized fruit of *Caesalpinia exostemma* (top), fruit split open to show intact seeds with translucent seed coat (middle), and longitudinally sectioned fruit to show dark-green embryos (cotyledons) in full-sized, immature seeds. D. Partly mature fruit of *Caesalpinia coriaria* longitudinally sectioned to show nearly mature seeds with whitening embryos (cotyledons) (upper two seeds) and less-mature seeds with green embryos (two seeds on lower right), and clear endosperm (between elongate thin embryos and seed coats). E. Nearly mature fruit of *Rourea glabra* (upper) and section through less-mature fruit showing green cotyledons and white fruit pulp (aril). F. Nearly mature, bright-green fruit of *Apeiba tibourbou* (left) and section through fruit (right) showing white, mature seeds imbedded in a brownish-yellow matrix. G. Maturing fruit of *Dioclea megacarpa* split open with one seed split (left) to show white insides. H. Sections through fruits of *Aphelandra deppeana* to show white, young seeds (left) and white, nearly mature seeds (right). All fruits from the lowland, deciduous forests of Santa Rosa National Park, northwestern Costa Rica, March 1980 (all scales in millimeters).

a non-trivial fraction of the material used to develop and fill a seed. However, they do not show what fraction of this photosynthetic activity is performed by chlorophyllous embryos and what fraction by maternal fruit tissue. This distinction is important because a fruit is parasite(s) and host combined in one complex structure. The offspring live in such a resource-limited environment that even very small amounts of resources from their own photosynthesis are likely to be of proportionately large value. When the developing embryo is chlorophyllous, several var-

iables are added to the already-complex interaction between the fruit and seeds. Fruit and seed shape are under selection to increase exposure of cotyledonary tissues; as fruit walls thicken or seeds become thicker in response to other selective pressures, a cost is incurred through deprivation of a chlorophyllous embryo of sunlight. The seeds packed into a spheroidal or thickly cylindrical fruit deprive each other of light. Fruit-developmental timing should also be influenced by chlorophyllous embryos; even rainy-season, cloudy daylight is adequate for photosynthesis

TABLE 1. Traits of 74 species of developing wild perennial plant fruits recorded on 8-10 March 1980 (mid dry season) in the lowland deciduous forests of Santa Rosa National Park, northwestern Guanacaste Province, Costa Rica.

	Fruit shape	Approximate number of seeds	Seed weight += >1 g - = <1 g	
CHLOROPHYLLOUS EMBRYOS				
Anacardiaceae				
	<i>Astronium graveolens</i>	Cylinder	1	—
Burseraceae				
	<i>Bursera simaruba</i>	Angular sphere	1	—
Combretaceae				
	<i>Combretum farinosum</i>	4-bladed flat disk	1	—
	<i>Terminalia chiriquensis</i>	Flat disk	1	—
Connaraceae				
	<i>Rourea glabra</i>	Ovoid sphere	1	—
Convolvulaceae				
	<i>Ipomoea carnea</i>	Angular sphere	4	—
	<i>Merremia umbellata</i>	Sphere	4	—
	<i>Merremia cissoides</i>	Angular sphere	4	—
Hippocrateaceae				
	<i>Hemiangum excelsum</i>	Broad-blade propeller	2-4	—
Leguminosae:				
	<i>Acacia collinsii</i>	Flattened cylinder	8-15	—
	<i>Acacia farnesiana</i>	Cylinder	10-15	—
	<i>Ateleia herbert-smithii</i>	Flat disk	1	—
	<i>Bauhinia unguolata</i>	Flat strap	5-10	—
	<i>Caesalpinia exostemma</i>	Flat strap	3-5	—
	<i>Caesalpinia coriaria</i>	S-loop flat strap	2-5	—
	<i>Cassia biflora</i>	Flat strap	5-15	—
	<i>Cassia emarginata</i>	Flat strap	20-40	—
	<i>Cassia hayesiana</i>	Cylinder	20-30	—
	<i>Centrosema plumieri</i>	Flat strap	6-10	—
	<i>Centrosema pubescens</i>	Flat strap	6-15	—
	<i>Crotalaria maypurensis</i>	Cylinder	10-15	—
	<i>Desmanthus virgatus</i>	Flat strap	10-15	—
	<i>Enterolobium cyclocarpum</i>	Flat disk	5-20	—+
	<i>Gliricidia sepium</i>	Flat strap	3-10	—
	<i>Haematoxylon brasiletto</i>	Flat strap	1-4	—
	<i>Piscidium carthagenensis</i>	4-bladed flat strap	1-4	—
	<i>Pithecellobium saman</i>	Flat strap	5-20	—
	<i>Phaseolus lunatus</i>	Flat strap	2-5	—
	<i>Prosopis juliflora</i>	Undulating flat strap	10-15	—
	<i>Pterocarpus robrii</i>	Flat disc	1	—
Malpighiaceae				
	<i>Banisteriopsis cornifolia</i>	Samara	1	—
Malvaceae				
	<i>Malva viscus arboreus</i>	Sphere	3-6	—
Ochnaceae				
	<i>Ouratea lucens</i>	Ovoid sphere	1	—
Polygonaceae				
	<i>Coccoloba venosa</i>	Sphere	1	—
	<i>Triplaris melaenodendron</i>	Shuttlecock	1	—
Rosaceae				
	<i>Licania arborea</i>	Ovoid	1	—+
Rubiaceae				
	<i>Calycophyllum candidissimum</i>	Cylinder	1	—
Sapindaceae				
	<i>Serjania schiedeana</i> ^a	Samara	1	—
	<i>Thouimidium decandrum</i>	Samara	1	—
Simaroubaceae				
	<i>Picramnia quaternaria</i>	Ovoid sphere	1	—
	<i>Simarouba glauca</i>	Flattened sphere	1	—+

TABLE 1. (Continued)

ACHLOROPHYLLOUS EMBRYOS			
Acanthaceae			
	<i>Aphelandra deppeana</i>	Ovoid sphere	4-8
Anacardiaceae			
	<i>Spondias purpurea</i>	Ovoid sphere	1-6
Annonaceae			
	<i>Sapranthus palanga</i>	Cylinder	8-15
Apocynaceae			
	<i>Tabernaemontana chrysocarpa</i>	Pear-shaped	20-100
Asclepiadaceae			
	<i>Matelea trianae</i>	Flanged ovoid sphere	200-300
	<i>Sarcostemma glauca</i>	Flanged ovoid sphere	100-200
Bignoniaceae			
	<i>Crescentia alata</i>	Sphere	200-400
	<i>Tabebuia rosea</i>	Cylinder	50-100
Cactaceae			
	<i>Opuntia elatior</i>	Sphere	20-50
Caricaceae			
	<i>Carica papaya</i>	Sphere	30-50
Cochlospermaceae			
	<i>Cochlospermum vitifolium</i>	Ovoid sphere	100-200
Elaeocarpaceae			
	<i>Muntingia calabura</i>	Sphere	300-500
Euphorbiaceae			
	<i>Hippomane mancinella</i>	Sphere	1-5
Flacourtiaceae			
	<i>Casearia arguta</i>	Sphere	4-10
Leguminosae			
	<i>Andira inermis</i>	Sphere	1
	<i>Dioclea megacarpa</i>	Flattened cylinder	1-5
Moraceae			
	<i>Ficus ovalis</i>	Ovoid sphere	200-300
Myrsinaceae			
	<i>Ardisia revoluta</i>	Sphere	1
Orchidaceae			
	<i>Brassavola nodosa</i>	Ovoid sphere	500,000
	<i>Encyelia cordigera</i>	Ovoid sphere	500,000
	<i>Laelia rubescens</i>	Ovoid sphere	500,000
Palmae			
	<i>Acrocomia vinifera</i>	Sphere	1
Passifloraceae			
	<i>Passiflora pedata</i>	Sphere	100-200
Rosaceae			
	<i>Hirtella racemosa</i>	Ovoid sphere	1
Rubiaceae			
	<i>Genipa americana</i>	Sphere	20-50
Sapindaceae			
	<i>Cardiospermum 11882^b</i>	Inflated angular sac	1
Sapotaceae			
	<i>Mastichodendron capriri</i>	Sphere	1
Solanaceae			
	<i>Cestrum nocturnum</i>	Sphere	2-6
	<i>Solanum torvum</i> X <i>S. ochraceo-ferrugineum</i>	Sphere	10-50
Sterculiaceae			
	<i>Guazuma ulmifolia</i>	Sphere	20-50
Tiliaceae			
	<i>Apeiba tibourbou</i>	Sphere	100-300
	<i>Leubea speciosa</i>	Ovoid sphere	15-30
Verbenaceae			
	<i>Lantana camara</i>	Sphere	1

^aDark-green seed coat, pale-green embryo.

^bDark-green seed coat, white embryo.

by fruit surfaces but only the intense sunlight from a dry-season, cloudless sky may be adequate for photosynthesis by embryos deep within a fruit. Translucence of the fruit and seed coat should be selected for, as will be traits that allocate and retain the carbon dioxide generated by the embryo; however, the benefits will have to be balanced against the loss of control over the embryo by the parent. One chlorophyllous embryo may be able to accumulate more reserves than can its chlorophyllous sibs, and it may be able to express its novel genotype more fully in competition with sibs for the resources from the parent.

I predict that facultative embryo chlorophylly, as might be expected in the outer layer of seeds in a many-seeded spheroidal fruit or in an insolated fruit

on a species that normally bears its fruits in shade, will be rarely encountered. Facultative chlorophylly would confound the very precise mechanisms that the maternal parent must have for resource allocation to seeds. Furthermore, I predict that the stomate-free seed coat will be found to be a container that confines the chlorophyllous embryo to its own microcosm and prevents it from freely parasitizing the carbon dioxide generated by the fruit.

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