CHAPTER 5

Dormancy and Germination

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DORMANCY, GERMINATION, AND ADAPTATION

The seed phase is the most important stage in the life cycle of higher plants as regards survival; dormancy and germination are natural mechanisms to ensure this. The seed is often well equipped to survive extended periods of unfavorable conditions, and the embryo is protected by one or several layers of other tissues. These include endosperm, perisperm, seedcoats, and fruit tissues, which protect the embryo from physical damage and nourish it (in the case of the endosperm); all contribute to spreading the seeds after abscission. As we shall see, these surrounding layers play an important part in the regulation of dormancy and germination. For many tree species native to the northern hemisphere, with seed maturing and dispersing in late fall to early spring, dormancy is an acquired trait to carry them over the winter conditions ready for germination next spring. Similarly, for seeds of tropical tree species maturing and dispersing during the dry, hot season, dormancy prevents germination until the arrival of the rainy season.

However, most tropical tree seeds have no dormancy and can germinate readily after seed fall, provided there is moisture available. Most recalcitrant seeds, because of the absence of maturational drying and the fact that embryo growth and germination processes constitute a continuous process, show no developmental arrest. In some species, such as *Hopea ferrea*, the radicle emerges with a mucilage-like coating, thereby protecting the radicle from drying out. However, seeds of some tropical and subtropical species have a seedcoat-imposed dormancy, for example, legumes. Additional types of dormancy in the seeds of tropical and subtropical tree species include combined seedcoat and embryo dormancy in *Podocarpus falcatus* (Wolf and Kamondo 1993); the mechanical restriction of seedcoat in *Podocarpus usambarensis*, and embryo dormancy in *Warburgia salutaris* (Msanga 1998); and morphophysiological dormancy in *Taxus mairei* and *Myrica rubra* (Chien 1997, Chien and others 1998). According to Msanga (1998), of the seeds of 122 indigenous tree species in Tanzania, 70 percent are known to be nondormant, 29 percent show seedcoat-related dormancy, and less than 1 percent display a double dormancy. In southeast Asia, seed dormancy has been attributed primarily to seedcoat problems (Hor 1993).

In the moist tropics, there is often no requirement for seed dormancy since the microclimate is always favorable to seed germination and seedling establishment immediately following seed dispersal (Wolf and Kamondo 1993). However, seedcoat dormancy is commonly found in the species growing in semiarid and arid areas of the Tropics. The degree of dor-

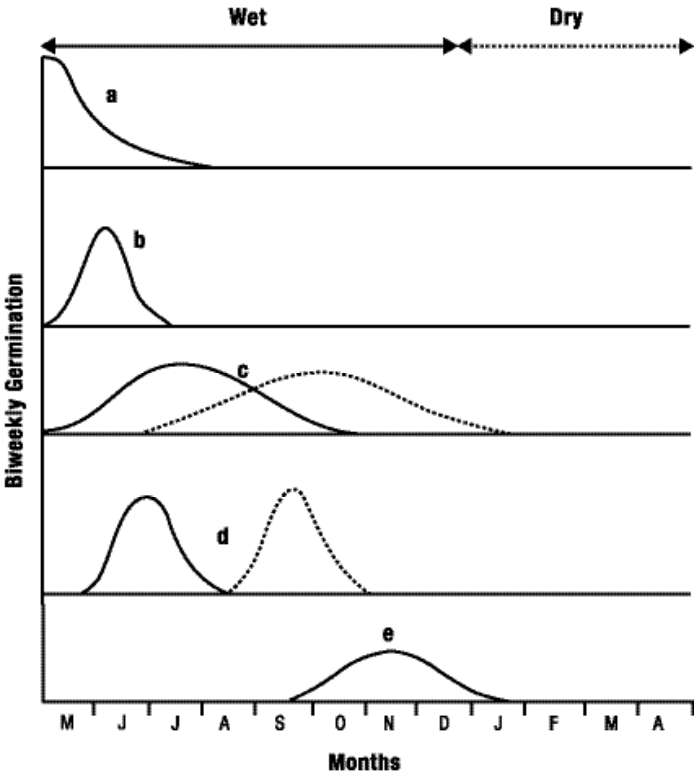

Fig. 1. Some seed germination strategies shown by tropical trees (adapted from Garwood 1986). The duration of the wet and dry seasons, and the timing of germination, are entirely arbitrary and may vary considerably between different forest types.

mancy among, and within, seedlots of the same species varies with provenance, crop year, and individual trees (Poulsen 1996, Wolf and Kamondo 1993). Although seeds of many tropical species have no dormancy, germination of some tree species is delayed as if they were dormant (i.e. *Diospyros kirkii, Moringa oleifera* Lam.) (Albrecht 1993, Msanga 1998). It is especially interesting to note that even seeds of many of the recalcitrant species exhibit delayed germination (i.e. *Allanblackia stuhlmannii, Strychnos cocculoides, Xymalos monospora, Ocotea usambarensis*) (Msanga 1998).

Apart from the rather clear-cut examples of coat-imposed dormancy as typified by many legumes, it is important to realize the great diversity seen in the synchrony of germination and the often wide range over which it can occur, even in the wet Tropics. This is illustrated diagrammatically in fig. 1. In the example illustrated there is a relatively long, wet period and a somewhat shorter dry period of 4 months. The shapes of the biweekly germination data (adapted from Garwood 1986) and their duration are somewhat arbitrary, but nevertheless illustrate five strategies.

What might be regarded as a recalcitrant strategy is seen in (a), where germination is almost immediate, high, and declines rapidly. It is evident that many pregermination events must have been taking place during development on the mother plant, as there is an absence of a lag phase in germination (seen in (b), however). The more typical pattern of dry dispersal, followed by imbibition and a single peak of synchronous germination in (b), might be considered representative of seeds without any significant coat-imposed dormancy. Such a sharply synchronous pattern might be seen in rapidly establishing forest species. The germination strategy illustrated in (c) represents the approach of maximizing germination in time, so as to widen the range of circumstances or locations for germination. The bimodal pattern may be seen as an "add on" benefit to maximize this strategy still further. The bimodal pattern shown in (d) achieves essentially the same temporal distribution as the unimodal pattern in (c), but with a greater element of synchrony. A cautious "failsafe" model is shown in (e), where germination timing is programmed to occur only after a number of quantal units of favorable hydrotime have been allowed to pass (Bradford 1996).

THE TROPICAL FORESTS OF THE WORLD

Tropical forests have been classified as moist evergreen, moist deciduous, and dry deciduous types, and account for, respectively, 20 percent, 10 percent, and 20 percent of the world's 2950 million hectares of forest (Borota 1991). Some of the principal trees of economic importance are presented in table 1, but the ecological value of other species should not be forgotten. Unfortunately these two objectives are often in conflict, although sustainable forestry requires integration of conservation and economic objectives.

Table 1
Important Tropical Trees, Listed Alphabetically by Geographical Region
(adapted from Borota 1991)

Africa	America	Australasia
Burkea	*Anacardium*	*Acacia*
Ceiba	*Andira*	*Afzelia*
Celtis	*Bombacopsis*	*Dalbergia*
Entandrophragma	*Caesalpinia*	*Dipterocarpus*
Khaya	*Carapa*	*Dryobalanops*
Maclura	*Cedrela*	*Eucalyptus*
Ocotea	*Guarea*	*Gonostylus*
Peltophorum	*Ocotea*	*Melaleuca*
Podocarpus	*Swietenia*	*Pterocarpus*
Triplochiton	*Virola*	*Shorea*
		Tectona

FACTORS AFFECTING GERMINATION AND SEED QUALITY

THE SCOPE AND OTHER REGIONAL DATA

As is perhaps evident from table 2, the topic is vast and scattered in many publications. Some tree seed manuals have appeared (Kamra 1989, Ng 1996, Poulsen and others 1998). Other reports are available on a regional basis for Australia, Brazil, Colombia, Costa Rica, Cuba, The Solomon Islands, and Thailand (Cavanagh 1987, Chaplin 1988, Figliolia 1985, Ortiz 1995, Pêna and Montalvo 1986, Quirrós and Chavarría 1990, Trivino and others 1990, Turnbull and Doran 1987, Uetsuki 1988). A manual presenting a practical framework for conducting field research on the reproductive biology of Asian forest trees has recently appeared (Ghazoul 1997), and in chapter 1 of this volume, Flores discusses aspects of tree seed biology.

Table 2

Flower, Fruit, and Seed Characteristics of Some Tropical Seeds by Family and Genus

R Denotes Recalcitrant Genera

Family	Genera	Flowers	Fruits, seed mass (mg)	Nodulation mycorrhiza	Dormancy
Anacardiaceae	*Spondias*[1]	Small, 4-5 united carpels;	Usually drupe; solitary seed		Yes:
		1 ovule;	with thin endosperm or		fleshy inhibitors?
	Schinus[2]	3 united	none; fleshy cotyledons		Woody inner coat?
	Schinopsis	carpels; 1 ovule	[1](3800) [2](30)		[2](10-30 days)
	Sclerocarya[R]				
	Lannea[R]				
Apocynaceae	*Aspidosperma cruenata*[1]	Large,	[1]Seed, undulator (871)		No?
	Hancornia[R]	2 united or free carpels,	follicarium, follicle,		
		paired fruits; fresh non	lomentarium		
		dehiscent fruit or dry,			
		splitting			
Bignoniaceae	*Tabebuia rosea*[1]	Showy bell- or funnel-	Many seed, 2 locule capsule		No?
		shaped corolla, single	[1](35) [2](5)		
	Spathodea	superior ovary;	amphisarcum, ceratium,		
	Jacaranda[2]	numerous ovules flat,	septicidal capsule		
		winged seeds			
Bombacaceae	*Bombacopsis quintata*[1]	5 sepals and petals—	[1]Seed, floater (33)		
	Ceiba pentandra[2]	sometimes fused; epicalyx	[2]seed, floater (74); [3]seed		[1]No
	Ochroma[3]	whorl.	with cotton-like fibers		[2,3]Yes—
	Bombax[4]	Many locules.	no or reduced endosperm		malvaceous affinities?
	Pachira[R]		amphisarcum, loculicidal or		[4]<15 ÞC damaging
			septicidal capsule [3](9)		
Boraginaceae	*Cordia alliodora*[1]	Uncoiling cymes:	[1]Fruit, helicopter (6)		
	Cordia aff. *panicularis*[2]	salver or bell-shaped,	4 (rarely 2) nutlets		No?-mostly herbs/shrubs?
		5 corolla lobes	or a drupe with or without		
		2 fused carpels—	endosperm [2](275)		
		2-4 locules			

Table 2 (continued)

Family	Genera	Flowers	Fruits, seed mass (mg)	Nodulation mycorrhiza	Dormancy
Burseraceae	*Aucoumea*[1]	Panicles of	[1](98)		
	Bursera	small unisexual flowers;	Drupe, sometimes		No
	Commiphora	sepals fused,	capsule,		
	Dacryodes	petals free,	no endosperm		
		3-5 carpels;			
		2-5 locules			
Leguminosae-		Legume, camara, samara	Legume, camara, samara		
Caesalpinioideae		more or less irregular	[1]5 seeds in thin pods	Nodulation	Yes
	Acrocarpus[1]	lateral petals (wings)	[2]6-10 seeds, dehiscent pods,	*Rhizobium*	[2]No, 11-20 days
	Afzelia[2]	calyx 5 unequal lobes;	(4000)		
		sepals free; short-toothed			
		calyx			
	Bauhinia[3]		[3]Dehiscent pod		[3]Some
	Cassia[4]		[4]Unassisted (9-32),		[4]Yes
			indehiscent pods		
	Caesalpinia				
	Delonix				
	Hymenaea[5]		[5]Indehiscent heavy pod		[5]Yes
			10 seeds (2000-6000)		
	Oxystigma				
	Parkinsonia[6]		[6]2-6 seeds, indehiscent pods		[6]Yes, 2-10 days
	Peltogyne		(76)		
	Swartzia				
	Tamarindus[7]		[7]1-10 seeds, indehiscent		[7]Yes, 40-50 days
			pods (714)		
Canellaceae	*Warburgia*[R]	Axillary flowers; small; 4-5	Berry - 2 or more seeds; oily		No, 15 days
		sepals, 10 petals; 2-5 carpels	endosperm (100)		embryo dormancy?
		single locule			
Casuarinaceae	*Casuarina*	Highly reduced, unisexual;	Hard woody fruits enclosed	*Frankia* and mycorrhiza	No, 11-23 days
		aggregate flowers cup-like	in bracteoles;		
		and naked; 2 fused carpels	wind dispersal samaroid nut,		
			(11)		
			No endosperm		

Table 2 (continued)

Family	Genera	Flowers	Fruits, seed mass (mg)	Nodulation mycorrhiza	Dormancy
Combretaceae	*Terminalia amazonica*[1]	Small and clustered; toothed	[1]Fruit, rolling autogyro (4)		No, 60-90 days
	Terminalia ivorensis[2]	calyx; no petals	[2]Fruit, rolling autogyro		
	Lumnitzera[R]		(160)		
	Laguncularia[R]		No endosperm,		
	Conocarpus[R]		variable cotyledons,		
			woody endocarp		
Dipterocarpaceae	*Anisoptera*				
	Dipterocarpus	Showy in racemes;	Single-seeded nut with wing	All mycorrhizal association	No
	Dryobalanops[1R]	3 carpels;	and membranous calyx;		
	Hopea[R]	3 locules;	no endosperm		
	Shorea[2R]	2 ovules: only	(pseudosamara)		
	Vatica	one developing	[1](4784)		
			[2](250-1075)		
Euphorbiaceae	*Croton*[1]	Condensed inflorescence;	Shizocarp or drupe,		Coat-imposed?
	Hura[2]	5 perianth segments;	mericarps dehisce after		[1]35-45 days
	Macaranga[2]	or lacking;	separation [3](29)		
	Manihot	and petals present;	abundant endosperm		
	Omphalea	locules open lengthwise;	[1]Woody endocarp		
	Ricinodendron	3 fused carpels,	[2]Coccarium, bacca,		
		3 locules, 1-2 ovules	polospermatium		
Lauraceae	*Ocotea*[1R]	Racemose or cymose;	Berry or drupe-like fruit,		[1]30-45 days
	Persea[R]	regular in multiples of 3;	enclosed variously by		Other genera
	Cinnamomum camphora[2]	poor petal/sepal differences;	perigynous part of flower		not recalcitrant?
	Sassafras randaiense[3]	single locule, single ovule	(cupule);		[2]Alternating temperatures
	Neolitsia ariabillima		no endosperm [1](666)		[3]Dormant - cold
					stratification
Lecythidaceae	*Barringtonia*[R]	Long spikes	Large fruits with fleshy		Coat imposed?
		showy and fluffy; 4-6 calyx	outer, hard/woody inner		
	Gustavia	and petal segments; 2-6	layer, and indehiscent;		
	Petersianthus	carpels and locules; 1 to	no endosperm		
		many ovules			

Table 2 (continued)

Family	Genera	Flowers	Fruits, seed mass (mg)	Nodulation mycorrhiza	Dormancy
Malvaceae	*Thespia*	Calyx of 5 sometimes joined sepals; epicalyx; 5 free petals; 5 or more carpels	Dry capsular or schizocarpic fruit, hairy seed, no endosperm		Yes?
Meliaceae	*Azadirachta*[1R]	Often cymose panicles; 3-5 free or united sepals also petals; ovary 2-6 locules	Capsule, fruit, berry; rarely nut		No: [1]30-40 days
	Guarea[2]				
	Trichilia[3R]		Winged: *Azadirachta* and *Guarea*; fleshy aril or sarcotesta in others		
	Carapa[R]				
	Cedrela[4R]		[1](200) [2](3500) [3](100-600) [4](20)		
	Entandrophragma[R]		[5](476) [6](490)		
	Khaya[R]		[2,3]loculicidal capsule [4,6]septifragal capsule		
	Melia[5]				[5]15-75 days
	Swietenia[6]				[6]4-30 days
Melastomataceae	*Astronia*	4-5 sepals, free petals, 1-14 carpels; 4-5 locules; 2 to many ovules	Berry or loculicidal capsule; small seeds; no endosperm		No
	Memecylon				
	Tibouchina				
Leguminosae-Mimosoideae	*Acacia*[1]	Erect or pendulous raceme; regular flowers:	Dehiscent or nondehiscent pods; 1-5; 10-12 seeds per pod; [1](7-169) [2](200-1970)	Nodulation: *Rhizobium*	Yes - [1]*A. nilotica* *A. tortilis;* No - [1]*A. senegal* See Tables 3 and 4
	Inga[2]				
	Pithecellobium[R]	5 sepals and petals, numerous stamens;			
	Albizzia[3]	5-10 stamens	[3]Nondehiscent pods; 8-14 seed per pod (83)		[3]Yes
	Prosopsis[4]		[4]Nondehiscent pods; 25 seeds per pod; sweet pulp (31)		[4]Yes, 10-30 days
	Pentaclethra[R]				

Table 2 (continued)

Family	Genera	Flowers	Fruits, seed mass (mg)	Nodulation mycorrhiza	Dormancy
	Faidherbia[5]		[5]Nondehiscent pod; 11-19 seeds per pod (76)		[5]Yes, 5-20 days
	Leucaena[6]		[6]Nondehiscent pod; 12-25 seeds per pod (50)		[6]Yes
	Parkia[7]		[7]Nondehiscent pod; 19 seeds with pulp (76)		[7]Yes
Moraceae	*Artocarpus*[R]	Small solitary flower	Variable fruits;		[1]Variable, see text
	Cecropia [1]	ovary with single ovule	pseudodrupe, sorosus,		[2]No, 45-60 days
	Castilla		synconium		
	Maclura[2]		with or without endosperm		
			[1](1)		
Myrtaceae	*Eucalyptus* [1]	Cymose (mostly)	[1]Unassisted (0.25-18)	[1]Mycorrhizae	No, 3-30 days
		or racemose; 4-5 (usually)	[2]Fleshy berry (120-6000)	[2]?	
	Eugenia [2R]	free sepals or	(Rarely drupe)		
	Melaleuca	reduced/absent			
	Metrosideros[3]			[3]Mycorrhizae	
		4-5 small free petals;	[3]Unassisted (0.057)		
	Syzgium[4R]	1-5 locules, 2-many ovules		[4]?	
			If dry: capsule or nut		
			[1]Capsiconium		
			[4]Polyembryonic (333)		
			Little or no endosperm		
Myristicaea		Small inconspicuous;	At maturity fibrous fruit		No
	Cephalosphaera	incapitate, fascicled or	splits open: 2-4 valves:		
	Myristica	corymbose inflorescence,	single large seed (dehiscent		
	Virola[R]	no petals, calyx or 3 united	berry) (800-3700)		
		sepals,	small embryo, large		
		single ovule; 1 or 2 carpels	endosperm with ingrowing		
			perisperm; aril		

Table 2 (continued)

Family	Genera	Flowers	Fruits, seed mass (mg)	Nodulation mycorrhiza	Dormancy
Leguminosae – Papilionoideae	*Andira* *Calopogonium* *Dalbergia*[1] *Gliricida*[2] *Lonchocarpus*[3] *Milletia* *Platylobium*[4] *Pterocarpus macrocarpus*[5] *Swartzia polyphylla*[R]	Irregular: lateral petals enclosed by standard in bud; 10 stamens	[1]Nondehiscent flat pod; 1-4 seeds; rolling autogyro (248) [2]Dehiscent pod, 3-10 seeds (90) [3]Fruit, rolling autogyro (143) [5]Fruit, undulator (337)	[4]Mycorrhizae	[1]No [2]No [5]Alternating temperatures best
Polygonaceae	*Triplaris*[1] *Coccoloba*[2]	Small flowers; solitary or grouped in raceme; 3-6 sepals - enlarge in fruit. No petals; 2-4 carpels in one locule	[1]Fruit, helicopter, (77); triangular nut [2](150-280) (Abundant endosperm)	[2]Mycorrhizae	No
Proteaceae	*Grevillea*	Raceme spike or head; ring of bracts, irregular: 4 perianth lobes; 2-4 scales (petals) alternate. Ovary with single carpel, 1 to many locules; persistent style	Wind dispersal (22) fruit a follicle with winged seed; no endosperm	Mycorrhizae	Coat imposed?
Sapotaceae	*Autranella* *Pouteria*[1] *Tieghemella*	Borne in fascicles, sepals free, two whorls of 2-4; 1 of 5. Equal number of petals; many fused carpels, many locules, single ovule.	[1]Berry (800-6250) 1-several seeds, oily endosperm, bony testa, large embryo		Coat-imposed?
Sterculiaceae	*Guazuma* *Triplochiton scleroxylon*	Regular in complex cymes; 3-5 sepals; 5 free or fused petals; ovary with 2-12 carpels; locules 2 or more ovules	Indehiscent dry capsule: 80-100 seeds or berry-like (310)		?

Table 2 (continued)

Family	Genera	Flowers	Fruits, seed mass (mg)	Nodulation mycorrhiza	Dormancy
Verbenaceae	*Gmelina*[1]	Irregular in racemose,	Stony 1-2 seeds. Drupe		No, [2]20-50 days
	Petitia	cymose inflorescence.	sometimes capsule, or		[2]Poor germination
	Premna	Calyx and corolla 4 or 5	schizocarp		
	Tectona[2]	lobed. Ovary of 2 (4,5)	[1](715) [2](10000)		
		fused carpels divided into 4	Little or no endosperm		
		(or more) locules. 1 ovule			
		per locule (false septa).			
Vochysiaceae	*Vochysia*	Irregular in compound	3-chambered capsule with		
		raceme; 5 sepals; petals 1-5,	winged seeds; no endosperm		No
		unequal size;			
		3 fused carpels, 3 locular			
		ovary			
Zygophyllaceae	*Balanites*[1]	Regular, solitary, paired or	Capsule slitting into 5 parts		Some, [1]7-30 days
	Bulnesia	cymes; 4-5 free sepals and	(or berry or drupe)		
	Guaiacum	petals; ovary of 5 fused	endosperm; seed pulp		
		carpels, 5 locules, 1 to many	[1](2800)		
		ovules.			

Data from: Albrecht 1993, Augspurger 1986, Foster and Janson 1985, Grubb and Coomes 1997, Heywood 1978, Jurado and others 1991, Spjut 1994.

INHERITED SEED CHARACTERISTICS

There are many factors influencing seed germination in general, and often the inherited effects on tropical and subtropical seed germination show differences from those of the temperate species. The following are considered important components of tropical and subtropical tree seed germination: seed germination mode, morphological and physiological constraints, the orthodox-intermediate-recalcitrance continuum, and seed polymorphism.

Seed Germination Mode

Three distinct seed germination behaviors can be recognized: epigeal, hypogeal, and intermediate (Msanga 1998). In addition, relatively unknown cryptogeal germination behavior was found in several tree and shrub species growing in the savanna tropics (Jackson 1974). Epigeal germination is considered to be fast and synchronous in contrast to the slower cryptogeal mode (Vazquez-Yanes and Orozco-Segovia 1993), which is more prevalent in larger seeds (Bazzaz and Pickett 1980). In a study of 64 leguminous species of the Amazon forest, hypogeal germination was observed only in large seeds that were more than 3.1 cm long, whereas in small seeds of less than 1 cm in

length, epigeal germination prevailed (Moreira and Moreira 1996). Hypogeal germination was also most prevalent in species associated with seasonally flooded habitats.

Figure 2 illustrates these different germination patterns with their descriptions.

Epigeal germination—This is the most common germination behavior and occurs in most coniferous and broadleaved species when cotyledons are forced above the ground by elongation of the hypocotyl, for example *Acacia, Afzelia, Diospyros, Jucbernadia, Juniperus procera, Pinus,* and *Tamarindus.*

Hypogeal germination—This type of germination occurs only in broadleaved seeds in which the cotyledons remain beneath the ground while the epicotyl elongates, as in *Agelaea heterophylla, Allanblackia stuhlmannii, Antiaris toxicaria, Khaya anthotheca, Ocotea usambarensis,* and *Quercus* spp.

Intermediate (between epigeal and hypogeal) germination—Two types may be distinguished. In the first, the seedcoat cracks and the radicle emerges through the scar end and develops into a taproot, then cotyledons unfold to release the developing shoot as typified by *Bauhinia petersiana, Clerodendrum cephalanthum,* and *Uapaca kirkiana;* in the second, the cotyledons remain inside the seedcoat but are lifted above the ground, as typified by *Dipterocarpus* and *Rhizophora*.

Cryptogeal germination—This type of seed germination, in which new shoots arise below the ground even though the seed germinated on the surface, occurs in several savanna tree and shrub species, for example *Combretum binderanum, C. molle, C. fragrans,* and *C. sericeum*. Apparently this type of germination evolved as an adaptation to an environment long subjected to annual burning, and serves to reduce water loss (Jackson 1974).

It is also interesting to note that, unlike the tree seeds in the temperate region, where the radicle always protrudes from the micropylar end of the seed unless germination is abnormal,

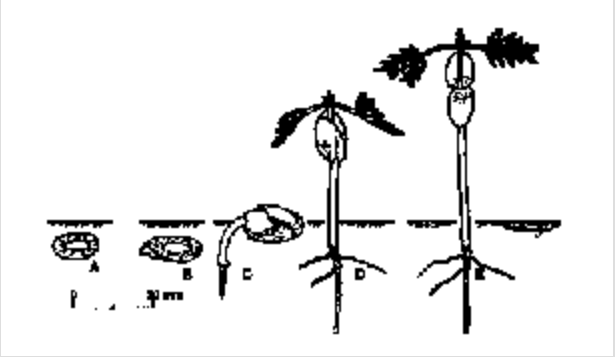

Fig. 2a. Epigeal germination (e.g. *Albizia lebbeck*) from time of sowing to full seedling development: A. at sowing; B. 5 days, C. 10 days, D. 15 day and 25 days after sowing (after Msanga, 1998).

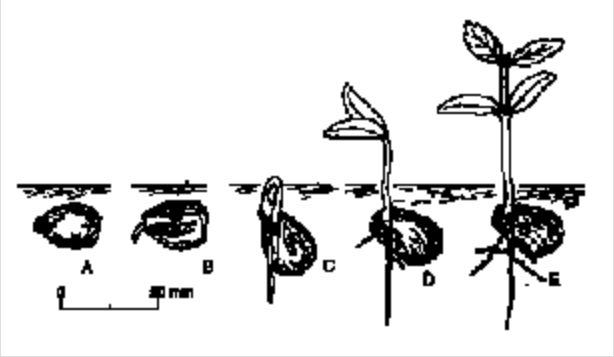

Fig. 2b. Hypogeal germination (e.g. *Vitex keniensis*) from time of sowing to full seedling development: A. at sowing; B. 14 days, C. 21 days, D. 28 days, and E. 35 days after sowing (after Msanga, 1998).

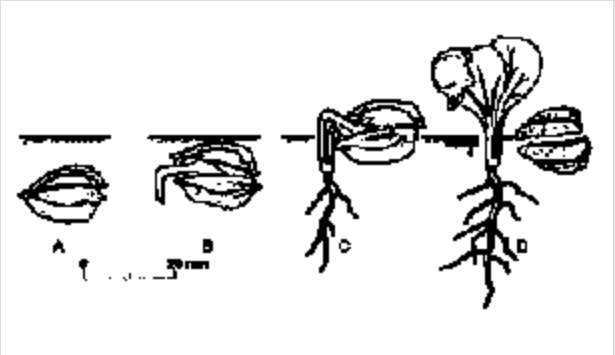

Fig. 2c. Intermediate germination (e.g. *Uapaca kirkiana*) from time of sowing to full seedling development: A. at sowing; B. 15 days, C. 20 days, and D. 30 days after sowing (after Msanga, 1998).

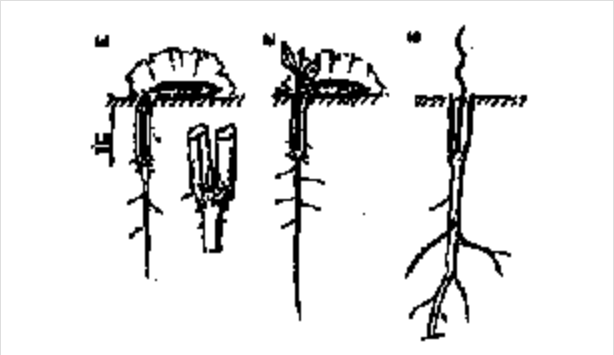

Fig. 2d. Crypotogeal germination (e.g. *Combretum sericeum*): January 4, 1969 (a); January 16, 1969 (b); June 8, 1969 (c) original plumule damaged, resulting in the growth of the cotyledonary axillary buds from the root crown. (after Jackson, 1974).

germination of some tropical tree species such as *Hopea ferrea* and *Markhamia lutea* have radicles that emerge from the middle of seeds (Msanga 1998, Pukittayacamee 1996).

Morphological and Physiological Constraints

The time of germination can be controlled not only by dormancy mechanisms (which are more strongly under genetic control) but also by timing of dispersal (which may be seen as more of a product environmental-genomic interaction). Thus, seed germination is ultimately the product of interactions such as flowering, pollination, seed development, seed dispersal, and seedling establishment. Developmentally the flower, fruit, and seeds constitute a morphological continuum and thus collectively exert a powerful influence on seed dormancy and germination. Primack (1987) has noted that the fruit wall may determine many aspects of seed germination. The fruit wall may split open at maturity in capsules, pods, and follicles, or it may persist as a hard protective layer in nuts, caryopses, and achenes. In addition, the fruit wall may envelop the seeds in soft, nutritious flesh, as seen in berries and pomes. Remnants of fruit structure that remain will determine its immediate physical and chemical environment, and have a dominant effect on germination. Finally, the seedcoat, which originated from the integuments of the ovule, also exerts an influence on germination.

In table 2 some differences are given which exist between families, genera, and even within species, as regards fruit size and type for some of the genera of tropical trees. The classification of fruit types has been taken from the recent revision by Spjut (1994), along with information from various sources of fruit weights. We accept that this table is likely to highlight the many gaps in our knowledge, but hope that it serves as an incentive for further study.

Most trees bear fruits with distinctive modifications for dispersal by explosive discharge, wind, or consumption by birds and mammals. It is noteworthy that Corner (1954) distinguished between megaspermous and microspermous seeds in the families of tropical plants, and that the megaspermous group included the families *Annonaceae, Bombacaceae, Burseraceae, Connaraceae, Dipterocarpaceae, Ebenaceae, Fagaceae, Guttiferae, Lauraceae, Lecythidaceae, Myristicaceae, Palmae,* and *Sapotaceae,* many of which are well represented in table 2.

The property of maintaining seed size reasonably constant within a species, while all other organs of the plant show high plasticity, has been attributed to the maintenance of continuity between generations (Harper and others 1970).

As can be seen in table 2, seed size varies over several orders of magnitude, with *Cocos nucifera* at one extreme (600 g) while *Eucalyptus* spp. (0.25 to 18 mg) and *Metrosideros* (0.057 mg) are at the other. It has also been noted that fleshy fruits are very common in most tropical rain forests, often in excess of 70 percent, while lower frequencies of 18 to 63 percent have been noted in the forests of Queensland, Australia (Willson and others 1989).

Dormancy and the Orthodox-Intermediate-Recalcitrant Continuum

We have refrained from defining dormancy and germination until this late stage for two reasons. First, although it is clear that these states are perhaps intuitively and morphologically evident, biochemical definitions are still lacking (Bewley 1997, Hilhorst and Torop 1997). Dormancy is generally regarded as a temporary suspension of visible growth (i.e. germination) and for many seeds the final phase of seed development involves significant water loss and entry into a metabolically inactive state. This definition, however, is framed to encompass man's important crop plants. If, when provided with suitable temperature, water, and oxygen, germination does not occur the seed is considered to be dormant. Traditionally dormancy is seen as being coat- or embryo-imposed, or a combination of the two. While coat-imposed dormancy is well researched in the legumes, and pretreatments to overcome this type of dormancy are discussed further, well-studied examples of the other dormancy imposition mechanisms are wanting for tropical tree species. Also, in view of the various syndromes mentioned in the Introduction, it might be more appropriate to consider tropical tree seeds as falling into three **germination** categories: coat-imposed germination, prompt germination, and delayed germination. These overlay, or perhaps integrate with, the three seed **storage** categories: orthodox, intermediate, and recalcitrant. Indeed, the question might be asked: to what extent in tropical tree seeds is maturational drying to low (orthodox seed) moisture contents an obligate or facultative attribute? The seeds of many tree species from the humid rain forests are recalcitrant and readily germinable upon falling on the ground as long as moisture is available (several Dipterocarps such as: *Dipterocarpus grandiflorus, Hopea ferrea, Shorea* spp.), while some of the species such as *Podocarpus macrophyllus,* and mangrove species such as *Rhizophora* germinate on the mother tree. Seeds of these species have the shortest longevity and complete their germination processes very quickly. In contrast, some recalcitrant seeds in Africa germinate very slowly (e.g. *Bersama abyssinica* attains 45 percent of its germination after 7 weeks and 70 percent after 10 weeks from sowing). The slowest recalcitrant seed germination was reported to reach 12 percent after 2 months

and 70 percent after 3 months from sowing (Msanga 1998). See also figure 1, which graphically illustrates these aspects.

In the subtropical region of Taiwan, recalcitrant seeds of several tree species like *Beilschmiedia erythophloia, Cinnamomum subavenicum, Litsea acuminata, Neolitsea variabillima,* and *Podocarpus nagi* require moist chilling treatment for maximum germination (Lin 1994).

For seeds of nondormant orthodox tree species such as *Acacia drepanolobium, Albizia anthelmintica, A. tanganyicensis, Eucalyptus camaldulensis* Den, *E. globulus, E. muculata, E. paniculata, Gliricida sepium, Samanea saman,* and most recalcitrant species, germination is usually completed between 3 and 14 days. Seeds of other tropical trees such as *Faidherbia, Cassia,* and *Delonix* have seedcoat-imposed dormancy and require some physical or chemical scarification treatment to overcome their dormancy. This allows water, oxygen, or both to enter the seeds and permits the embryo to overcome the mechanical restriction of surrounding tissues. Seedcoat-imposed dormancy is the major cause of many tropical tree seed germination problems and is discussed further in the section entitled Pretreatments to Overcome Dormancy.

Seed Polymorphism

In general, the frequency distribution of seed size and shape from either single plants or populations is a continuous distribution, normal or skewed. In plants showing seed polymorphism, two or more sharply defined distribution patterns are seen (Harper and others 1970). Attributes such as seed size, shape, dormancy, or internal structures are some of the forms in which polymorphism may be manifested.

For example, three seed types are seen in the legume *Ononis sicula* of the Israeli desert, whose seeds are polymorphic in color, size, weight, and water permeability. South American species of *Ormosia* produce both red and bicolored (black and red) seeds, the production of which appears to be highly variable. While the red seeds are susceptible to bruchid attack, the bicolored seeds are highly toxic and rarely attacked by bruchids (Van Staden and others 1989).

Seedcoat color changes are often associated with the onset of impermeability during seed maturation and there is evidence that seedcoat color is controlled by a single gene (Egley 1989). The adaptive value of this polymorphism is clearly evident: orange seeds of *Platylobium formosum* were seen to be less dormant than black seeds when studied over two successive years (Morrison and others 1992).

These workers also studied the dormancy patterns of some common Australian leguminous species, and showed that seed weight and volume were significantly related to the properties of nondormant seeds. Three groups were distinguished: those with a relatively small nondormant fraction at maturity (0 to 10 percent) which was maintained through time; those with a relatively large nondormant fraction (10 to 40 percent) which maintained dormancy over time, and those that possessed a relatively small nondormant fraction whose dormancy decreased over time. To what extent the above patterns are evident in tropical tree species remains to be determined. The presence of two or more distinct seed types in fruits is well documented in herbaceous species, e.g. *Xanthium* (Harper and others 1970). Augspurger and Hogan (1983) have noted that *Lonchocarpus pentaphyllus* has mature indehiscent fruits that may contain one, two, and three (rarely four) winged seeds; while this had clear implications for dispersal, the influence on germination remains unknown. Variable numbers of seeds per fruit were also noted for *Platypodium elegans, Dalbergia retusa,* and *Pterocarpus rohrii,* but again there is no clear evidence how this polymorphism may influence germination. That different sizes of seed may show marked differences in germination is well known: large and medium-sized seeds of *Syzgium cumini* gave better germination than smaller seeds (Ponnamal and others 1992); seed size did not influence germination percentage in *Virola koschnyi,* although large seeds produced more vigorous seedlings (Gonzalez 1993).

Sometimes the pattern observed is not entirely consistent. Roy (1985) showed that although the germination index for small seeds of *Albizia lebbeck* (L.) Benth. was greater than for large seeds, the actual percentage germination and seedling vigor were greater for larger seeds. This contrasts with another study (Prem Gupta and Mukherjee 1989) where 62 percent germination was recorded for large seeds (0.1 g) of *A. lebbeck* as against 74 percent for smaller seeds (0.08 g).

The germination of three weight classes of *Acacia melanoxylon* R. Br. (ranging from 0.0099 to 0.021 g) varied from 55 percent for lighter seeds to 95 percent for the heavier cohort (Gomez Restrepo and Piedrahita Cardona 1994).

Seed Maturity and Postharvest Handling

Apart from the above inherited characteristics that may influence germination, there are environmental influences and factors within the control of the seed scientist which fall under this heading. Some of these have been identified as: ecological conditions of the mother tree, seed collection date, seed quality and treatment, seed storage (discussed in chapter 3 of this volume), and seed germination tests. All seeds, whether they are orthodox or recalcitrant, require timely collection at or near their full maturity, then careful handling from collection to storage to obtain maximum physical and physiological quality. However, a wide range of reproductive patterns is seen in tropical trees. Flowering and fruiting patterns may be contin-

uous and predictable; show some seasonability (using environmental ones such as photoperiod, temperature, and drought); or be somewhat erratic. In dipterocarps it has been noted that flowering and fruiting may occur once every 2 to 3 years, and in some species may occur only every 11 years (Jansen 1974); sometimes only a third of the forest population may seed at any one time (Turner 1990). In addition, the number of flowers that develop into mature fruits can vary enormously, not only in a species-specific manner but also from year to year. Flower and fruit abortion can be considerable. For example, in *Ceiba pentandra* less than 0.1 percent of flowers mature into fruit, and only 10 percent of initiated fruits mature (Stevenson 1981). Immature or incompletely dried seeds have long been known to affect seed germination and vigor, and the choice of an optimal collection time is often a compromise between several factors. If flowering and fruiting are protracted, no one harvest time will provide seed of uniform maturity. Mahedevan (1991) has reported that tree-to-tree variations in fruiting and seed maturation in *Acacia nilotica, Albizia lebbeck,* and *Azadirachta indica* militated against a single collecting time. Marked genetic influences may also operate, as seen in the provenance trials of *Acacia mangium* from 20 localities, which yielded wide variations in seed characteristics and production (Bhumibhamon and others 1994).

Often, features such as fruit or wing color may provide useful indicators of seed maturity and germination. For *Gmelina arborea*, yellow and yellow-green fruits gave higher germination than green fruits (Mindawati and Rohayat 1994), while in *Shorea pinanga* and *S. stenoptera,* harvest of fruits with fully brown wings greatly improved final germination (Masano 1988). The narrow window for optimal harvest was shown by the study of Kosasih (1987) on *Shorea ovalis*. Harvests made at 9, 10, and 11 weeks, during which time coat changes occurred, showed 13 percent, 25 percent, and 93 percent germination, as well as more rapid germination. External signs of fruit ripeness, and suitable postharvest handling techniques, have been reported for 18 tree species from Colombia including *Bombacopsis quinata, Calophyllum mariae, Cordia allodorata, C. gerascanthus, Didymopanax morotonii, Jacaranda copaia, Tabebuia rosea, Virola* spp., and *Zanthoxyllum tachuelo* (Trivino and others 1990).

The potential for insect attack exists at any stage of seed production, and seed predation by insects causes the selective abscission of young fruits. A stand of *Cassia grandis* aborted 95 percent of initiated fruit, 81 percent of which were seen to be insect damaged (Stevenson 1981). For basic information on insect attack of orthodox seeds during storage the reader is referred to Howe (1972), while Birch and Johnson (1989) discuss seed predation specifically in the legumes. Field studies indicate that seeds may be subjected to seasonal attack, especially at the peak maturation period. Information is available on weevil attack in dipterocarps (Khatua and Chakrabati 1990, Kokubo 1987). Postfertilization weevil attack in *Syzgium cormiflorum* was reported to be as high as 70 percent (Crome and Irvine 1986). Sometimes insect attack is restricted to external pulpy tissues and does little harm (Eusebio and others 1989). Postdispersal seed mortality of 30 to 35 percent for *Virola nobilis* was accounted for by insect attack (Howe 1972), while a figure of 25 percent has been given for *Ocotea tenera* fruits on the parent tree (Wheelwright 1993).

A number of *Bruchus* spp. attack fruits in the field and are brought into storage with ripe seeds. Attacks on *Acacia* spp. have been especially well documented (Hedlin and Eungwijarnpanya 1984), while the genus *Caryedon* is prone to attack *Combretum, Cassia,* and *Acacia* spp. (Howe 1972). Eungwijarnpanya and Hedlin (1984) and Abdullah and Abulfatih (1995) have reported insect damage on species of *Acacia, Albizia, Bauhinia, Cassia, Dalbergia, Dipterocarpus, Shorea,* and *Tectona*. Johnson and Siemens (1992) have recorded bruchid attacks on *Acacia farnesiana* and *Pithecellobium saman* in Ecuador and Venezuela, while large-scale attack on seeds of *Virola surinamensis* by C*onotrachelus* weevils was observed around fruiting trees by Howe and others (1985). In some instances, toxic seed constituents may significantly limit seed predation by insects, such as *Pentaclethra*. Central American woody legumes form two natural groups by seed weight: the mean seed weight of 3 g in 23 species that have toxic seed constituents and are not attacked by bruchid beetle larvae, and the mean seed weight of 0.26 g in 13 species that are attacked by bruchid beetles (Harper and others 1970).

Interactions between insect and fungal damage may operate additively in some cases. Damage was found to range between 50 percent in November and over 70 percent in February for seeds of *Albizia lebbeck* collected in Madhya Pradesh (Harsh and Joshi 1993). A general account of seed fungi may be found in Baker (1972) and Mittal and others (1990). Both recalcitrant and orthodox seeds harbor fungi, which may have serious impact on germination. Mycock and Berjak (1990) examined seven recalcitrant crop species and found a spectrum of fungal contaminants in all; fungal proliferation was exacerbated by storage. Fungi were also evident in the orthodox seeds of the tropical tree species *Albizia, Cedrela, Entandrophragma, Gmelina, Khaya, Leucaena, Maclura, Terminalia,* and *Triplochiton* (Gyimah 1987). A diverse and abundant mycroflora were found to be associated with six species of *Eucalyptus* investigated by Donald and Lundquist (1988). Hot water treatments (50 °C), surface sterilization (10 percent sodium hypochlorite), or fungicidal treatment (captan) were effective in reducing fungi and increasing germination. Physical sieving alone, whereby fine chaff was removed from seed lots, was able to reduce fungal

contamination appreciably. Under field conditions, ants were seen to exert a positive effect on seed germination in *Hymenaea courbaril* by removing pulpy and fungus-infected pulp (Oliveira and others 1995). Further details on seed pathology may be found in chapter 6, by Old and others. Recalcitrant fruits are commonly collected before they reach full maturity due to their short collecting windows. Consequently, they must be handled with great care in transporting and processing to limit fungal and insect attack and maximize germination. The effect of postharvest handling on the quality of provenances of recalcitrant seeds of *Azadirachta indica* has been reported (Poulsen 1996). Immature or improperly processed seeds have long been known to affect seed germination and vigor. Collection of fruits/seeds from the ground is convenient and economical, but usually results in poor quality seed if improperly timed (Willan 1985). In Brazil, emphasis has been placed on reducing transporting time of fruits of *Gmelina arborea* in sacks to prevent losses in germinability (Woessner and McNabb 1979). Willan (1985) suggested that critical factors for recalcitrant fruits were ventilation, temperature, moisture content, nursery practices, and careful handling in long-distance transport.

The processing of fleshy fruits requires timely extraction to avoid fermentation. All recalcitrant fruits should be dried in the shade with good ventilation. Seeds of some recalcitrant species like *Bersama abyssinica* and *Trichilia emetica* require 4-day postharvest ripening before processing (Msanga 1998). A period of postharvest ripening was also required by *Shorea siamensis* and *Shorea roxburghii* (Panochit and others 1984, 1986), as well as for *Persea kusanoi*, *Neolitsea acuminatissima*, and *Cinnamomum philippinise* (Lin 1994, Lin and others 1994). Handling is especially critical for germinating intermediate and recalcitrant fruits/seeds requiring slow drying under shade and cool temperatures (e.g. *Swietenia macrophylla*), then washing and macerating to remove pulpy tissues.

It sometimes may be difficult, particularly in smaller-seeded species, to distinguish between fully developed or incompletely filled seeds. Density separation, using solutions of either polyethylene glycol or potassium carbonate, provides a convenient means of effecting separation between "floaters," "sinkers," and debris (Hurley and others 1991, Tsuyuzaki 1993).

PRETREATMENTS TO OVERCOME DORMANCY

Dormancy in tropical and subtropical tree seeds is predominantly seedcoat imposed. Various effective and practical treatments have been developed to break this dormancy. Nicking, hot water soaking, and physical or acid scarification have all been used to good effect with the seeds of the many legume species of tropical and subtropical origin.

The role of the seedcoat in regulating imbibition is well known in legumes, and differences in seedcoat permeability resulting from maturational factors, mechanical damage during harvest, or scarification treatments may all impinge negatively on germination by causing imbibition injury (Powell and Matthews 1979, 1991). In the tropical forage legume *Calopogonium mucunoides*, the water absorption pattern was characteristic for each individual seed lot, and higher imbibition rates were associated with seeds of lower quality (Souza and Marcos-Filho 1993).

LEGUME SEEDCOAT STRUCTURE

The impermeable properties of the legume seedcoat to water or gases, and its property of providing a mechanical restraint to the embryo, are achieved by a combination of structural and/or chemical properties, which have been elucidated by anatomical and ultrastructural studies. While the seedcoat is seen as a hindrance to uniform and rapid germination, it should be remembered that the coat nonetheless performs the critical functions of regulating water uptake, providing a barrier to fungal invasion, and reducing leakage from the embryo during imbibition. As Hanna (1984) noted, most investigations have unfortunately concerned themselves with finding mechanisms for improving germination rather than determining mechanisms involved in the process.

Although the topic has been extensively investigated for more than four decades (Bhattacharya and Saha 1990, Dell 1980, Hyde 1954, Maumont 1993, Serrato-Valenti and others 1995), it is perhaps necessary to bring the results of these many reports together in one place. One recent useful review on this topic is that of Egley (1989).

Figure 3 illustrates some of the relevant features of the legume seedcoat. It is important to remember that while impermeability is seen in all three legume families, there are many differences, and not all legumes necessarily have a significant coat-imposed dormancy (see also table 2). Fresh seeds of *Gliricidia* and *Xylia* germinated readily (Iji and others 1993), and although seeds of *Hymenacea courbaril* showed hard coats, good germination was reported at 23 °C in soil, without any scarification treatment. Developmental events during late maturational drying are critical to the acquisition of impermeability. All sites that were open during early development, such as the hilum, micropyle, and chalazal pore, seal up during the late stages of seed drying. At 20 percent water content, and below, the epidermis of the seedcoat is considered to become markedly impermeable.

The cuticle on the seed surface is the first line of impermeability, although it is no longer considered to be the major or sole barrier to water entry. Below the cuticle lie thick-walled, tightly packed rows of columnar cells (Palisade or Malpighian cells) which completely enclose the embryo except for the hilum, micropyle, and chalazal pore; these cells are considered to play a major role in preventing water ingress. During the final stages of maturational drying, seed shrinkage intensifies the process of compression of these cells, and the occlusion of their lumen, along with impregnation of the wall by such substances as suberin. Typically the hilum is responsible for further seed drying, acting as a hygroscopic valve by closing at high atmospheric relative humidity (r.h.), thereby limiting water vapor uptake. Likewise, by opening when atmospheric r.h. is low, the hilum permits further water loss from the seed. Differential tensions between the palisade and counter-palisade cells are thought to cause hilar movement (fig. 3D). Caesalpinoid and mimusoid legumes generally lack

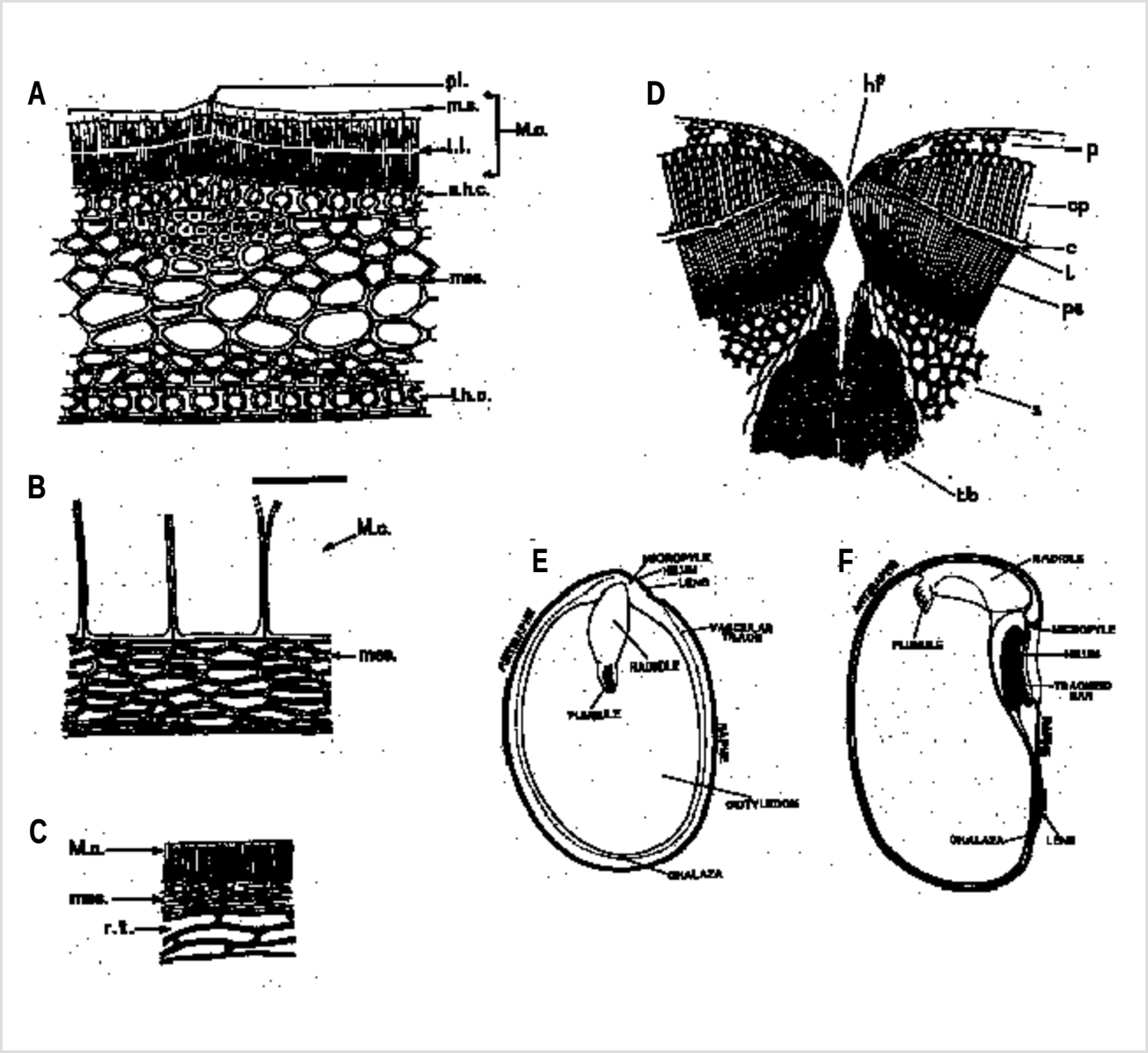

Fig. 3. Microscopic and macroscopic morphological details of some legume seeds and testae: (A) *Acacia galpinii*, (B) *Inga acreana*, and (C) *Pithecellobium cochleatum* (Reproduced from Maumont 1993); (D) Section through hilar region of *Lupinus arboreus* (Reproduced from Hyde 1954); medium longitudinal sections through raphe-antiraphe regions of (E) *Acacia farnesiana*, and (F) *Schotia brachpetala* (Reproduced from van Staden and others 1989). Abbreviations: pl. = pleurogram; m.s. = mucilage stratum; l.l. = light line; e.h.c. = external hourglass cells; M.c. = Malpighian cells; mes. = mesophyll; i.h.c. = internal hourglass cells; r.t. = resinous tissue; h.f. = hilar fissure; p = palisade; c.p. = counter-palisade layer; P.e. = palisade epidermis; s = spongy (mesophyll); t.b. = tracheid bar.

the complex hilum seen in the papilionids, and so the water regulation system needs further clarification. Below the Malpighian cells there is sometimes a squat layer of hypodermal "hourglass" cells with thickened walls (fig. 3A), but this is not universal, and sometimes compressed mesophyll cells are seen (figs. 3B and 3C).

These cells, which may have thick or hard pectic layers, have also been implicated in restricting water uptake or movement. Inner "hourglass" cells are the last cell type in "typical" legume coats (fig. 3A), but in other genera other cells may be seen, e.g. resinoid tissue *Pithecellobium* (fig. 3C).

The "hourglass" cells do not develop below the strophiolar plug region (also called the lens), and sometimes thin-walled parenchyma cells create a natural point of weakness (e.g. *Albizia* and *Acacia*). Other cell types have been reported here, such as the "white cells" of *Leucaena leucocephala* (Serrato-Valenti and others 1995), and these may be important in the early aspects of water movement into the seed. The long, narrow Malpighian cells in the strophiolar (lens) region have a greater tendency to split when subjected to heating, physical, or chemical treatments, but the exact manner of lens rupture may seem to be legume-specific. Irreversible lens rupture seems common in mimusoid legumes, but not in the papilionids; the vascular bundle below the lens and its association with coat rupture needs to be considered in the overall process. The "ejection" of lens cells is characteristic of *Albizia* given heat treatment, compared to a more controlled lifting in *Acacia.* Finally, the chalazal split, which may be geographically quite distinct from the hilum, may lose its sealing deposit or it may break down naturally; subsequent water uptake may cause differential cell expansion and buckling of the wall layers of the testa.

Often, once the seedcoat has been breached and imbibition has occurred, germination may still be impaired. This has been variously attributed (but not proven) to hormonal aspects and the requirement for other germination signals (e.g. light). Frequently, darkening (tanning-type reactions), associated with maturation drying is considered to play a role in the impermeabilization process. To what extent this is a regulated developmental event occurring at a specific, particular, water content (like LEA proteins) or is purely a "last ditch" response associated with final loss of cellular integrity, is unknown. The process does seem to show striking parallels with peroxidase-initiated free-radical polymerization of lignins (and suberins) seen in xylem vessel differentiation (Fukuda 1996, McCann 1997). There is some evidence that the rates of maturational drying can influence seedcoat properties (Egley 1989), and hence coat-imposed dormancy. Nutrient status, cytokinins, and abscissic acid have also been suggested as additional elements involved in seedcoat development (Egley 1989).

TREATMENTS TO BREAK SEEDCOAT DORMANCY

Nicking

This treatment involves cutting the seed at the distal (cotyledonary) end with a sharp tool like a scalpel, a razor blade, or a large nail clipper. The treatment is practical for treating small quantities of seed for testing or research purposes, but is time consuming and laborious. It has been found effective in releasing the dormancy of *Acacia tortilis, A. seyal, Albizia gummifera, Brachystegia spiciformis, Delonix elata, Faidherbia albida, Leucaena leucocephala, Maesopsis eminii,* and *Terminalia* spp. (Msanga 1998, Wolf and Kamondo 1993).

Soaking in Water

This is the simplest treatment to give the seeds an early start in the germination process. It has effects not only on the activation of enzymes and mobilization of reserves, but also on the softening of hard seedcoats and leaching out of chemical inhibitors. Soaking in water for 2 to 48 hours has been reported to improve seed germination of many tropical tree species such as *Acacia mearnsii, A. melanoxylon, A. nilotica, Adenanthere mirosperma, Albizia amara, A. procera, Grevillea robusta, Trewia nidiflora,* and *Pinus caribaea* (Matias and others 1973). Aerated, cold-water soaking for 28 days at 1.1 °C was found to be effective in breaking moderate dormancy and enhancing germination of *Pinus taeda* seeds (Barnett and McLemore 1967). In contrast, Andressen (1965) found cold, distilled-water soaking at 3 °C for 7 to 14 days depressed the germination of *Pinus strobiformis* seeds of northern Arizona and northern New Mexico. Experience of the USDA Forest Service's Eastern Tree Seed Testing Laboratory indicated that long periods of soaking (7 to 14 days) is apparently injurious to coniferous seeds unless they are soaked in aerated water (Swofford 1965).

Alternate soaking and drying of agricultural seeds has been studied as a treatment to improve seed germinability and increase crop productivity (Basu and Pal 1980, DasGupta and others 1976). Yadav (1992) investigated the influence of various soaking-drying treatments on the subsequent performance of *Tectona grandis* in field plantings. Germination was most rapid for alternate soaking and drying treatments, while the highest total germination occurred with 6 or 8 days of uninterrupted soaking. Soaking treatments of 10 and 12 days were deleterious to germination, and seeds receiving the soaking-drying treatments gave better germination than the control. The above results are fully supported by an earlier study on *T. grandis* which showed 12-hour alternate soaking and drying

for 1 month improved germination for 36 provenances of seed. Most seeds germinated in a single flush, but for five sources, two to three successive flushes were observed at 9- to 10-month intervals (Bedell 1989). Apparently, as pointed out by Berrie and Drennan (1971), this treatment was extensively reviewed earlier by Kidd and West. They suggested that soaking and drying treatments can have varying effects on germination depending on the rate of drying, the species tested, and the duration of the soaking. Berrie and Drennan (1971) found that the beneficial effect of the treatment was some advancement of the onset of germination, due probably to slight changes in the seed covering and also to the initiation of metabolic events which could withstand the drying. They claimed that there was little harmful effect from drying if it was carried out before cell division and enlargement had begun, but some of the chemical changes induced by soaking cannot be reversed to the original dry seed condition by drying. When embryo growth is apparent, some embryo damage will usually result from the drying. The physiological basis of the beneficial effects of soaking and drying treatment is not yet well understood (Basu and Pal 1980). Based on the research results on agricultural crop seeds from Basu and Pal (1980), the effect of soaking and drying was primarily prophylactic; it seemed to be able to eliminate the cause of subsequent seed deterioration rather than to repair the damage already inflicted to the bio-organelles. Nevertheless, this interesting seed treatment deserves further study.

Hot Water Soaking

This treatment involves soaking seeds in water at 40 to 100 °C depending on the species and seedcoat thickness, for a specific period of time or until the boiling water cools to room temperature. For example, *Celtis africana, Cordia sinensis* (stored seeds), and *Melia volkensii* seeds require soaking in water at 40 °C and then cooling down to room temperature. For *Acacia nilotica* and *Tamarindus indica*, pouring 80 °C water over the seeds in a container, followed by a soaking for 24 hours, was found to be effective (Albrecht 1993). Pouring 100 °C water over the seeds of *Adansonia digitata, Calliandra calothyrus,* and *Sesbania sesban*, with continued soaking as the water cooled off for 24 hours, was reported effective in breaking seedcoat dormancy (Albrecht 1993). In contrast, a brief soak in 90 °C water for 1 minute resulted in good germination of *Acacia mearnsii* and *A. melanoxylon* seeds (Albrecht 1993), while 30 seconds of soaking in boiling water overcame seedcoat dormancy of *Acacia mangium* seeds (Bowen and Eusebio 1981). This treatment is the quickest, cheapest, and simplest method for releasing seedcoat dormancy of many tropical species in operational applications.

Acid Scarification

This treatment is effective and practical for breaking seedcoat dormancy of many tropical species, but it is not commonly used due to its cost, the risk, and safety precautions involved. The treatment requires soaking seeds in 95-percent pure (1.84 specific gravity) sulphuric acid in an acid-resistant container such as thick plastic, for various periods depending on the species, draining the acid over a screen, then washing and drying the seeds. The drained acid can be re-used. The effectiveness of the treatment can be judged by the high percentage of swollen seeds and their dull, pitted appearance (Bonner and others 1974). According to Swofford (1965), for proper application of acid scarification the seed moisture content should be less than 10 percent because higher moisture content makes the action of sulphuric acid more violent, with possible seed injury.

The acid scarification can be applied either at room temperature or in a heated condition (70 °C) (Tietema and others 1992). The timing of this treatment is critical, as the soaking period and the postsoak washing have to be precisely controlled to avoid seed injury. Table 3 provides details of acid scarification treatment periods for some tropical tree species from the published literature.

Soaking in Hydrogen Peroxide Solution

Soaking seeds in 5 to 30 percent H_2O_2 for 30 minutes effectively reduced seed-borne microflora and stimulated germination of *Vangueria infausta* (Msanga and Maghembe 1989) and *Albizia schimperana* (Msanga and Maghembe 1986). For improved germination of camphor (*Cinnamomum camphora*) seeds, they must be soaked in 15 percent H_2O_2 for 25 minutes (Chien and Lin 1996).

Physical Scarification

This treatment can be achieved either manually, for small quantities of seed for laboratory testing or research purposes, or by mechanical equipment like the "seedgun" (Mahjoub 1993, Poulsen and Stubsgaard 1995, Msanga 1998), the Forberg mechanical scarifier (Piotto 1993), or the cement mixer (Albrecht 1993). When small quantities of seed are required, the "glow burner" or "hot wire" is an effective and efficient device for many tropical seeds (Poulsen and Stubsgaard 1995, Msanga 1998). When large quantities of seed are needed for operational sowing, use of a seedgun was also reported to be effective and efficient (Mahjoub 1993, Poulsen and Stubsgaard 1995, Msanga 1998).

A sandpaper-lined commercial mill was used by Todd-

Table 3

Some Recommended Acid Scarification Treatment Periods for Breaking Seedcoat Dormancy in Tropical Tree Species

Species	Acid condition	Treatment period (min)	Reference
Acacia auriculiformis	R	30	Pukittayacamee 1996
A. burkei	H	4	Tietema and others 1992
A. erioloba	R	3	Tietema and others 1992
A. hebeclada	R	120	Tietema and others 1992
A. karroo	H	2	Tietema and others 1992
A. nilotica	R	5-75	Zodape 1991
A. nilotica	H	9	Tietema and others 1992
A. tortilis	R	90	Tietema and others 1992
Albizia procera	R	15	Pukittayacamee 1996
A. lebbeck	R	5-75	Zodape 1991
Burkea africana	R	40	Tietema and others 1992
B. racemosa	R	5-75	Zodape 1991
Celtis africana	R	5	Tietema and others 1992
Cassia siamea	R	15	Kobmoo and Hellum 1984
C. nodosa	R	20	
C. fistula	R	20	
Leucaena leucocephala	R	20-60	Cruz and others 1995
Parkinsonia aculeata	R	5-75	Zodape 1991
Peltophorum africanum	R	60	Tietema and others 1992
P. lasyrachi	R	15	
P. pterocarpum	R	30	Pukittayacamee and others 1996
Terminalia brownii	R	60	Specht and Schaefer 1990

R = room temperature; H = heated to 70 °C.

Bockarie and others (1993) to uniformly scarify seeds of *Cassia sieberiana* and produce a uniformly high germination, equal to that of sulphuric acid treatment. Significant differences were noted among parent trees as regards the best pretreatments employed (table 4). As Gosling and others (1995) have noted, there is no real consensus on what constitutes the "best" method of pretreatment; intrinsic biological variation between species, seedlots, and individual seeds is doubtless responsible for much of this. Sulphuric acid treatments were successful in improving the germination of all 20 leguminous species tested including *Acacia albida, Albizia lebbeck, Caesalpinia decapetala, Delonix regia, Leucaena leucocephala,* and *Parkinsonia aculeata*. Dry heat (60 to 100 °C), a little-used method in general, was effective in 68 percent of species tests, whereas mechanical scarification was effective for 90 percent of the tested species.

An especially promising advantage from the use of the acid scarification technique has recently been suggested (Duguma and others 1988, Some and others 1990, Todd-Bockarie and others 1993). This involves acid scarification, washing and drying at a central facility, followed by distribution to nurseries and storage for later use. Storage for up to a year may be possible for prescarified seeds of *Acacia albida, A. nilotica, Bauhinia refescens, Parkia biglobosa, Faidherbia albida, Leucaena leucocephala*, and possibly *Cassia sieberiana*.

Sometimes the choice of method may be a compromise between labor intensiveness and seed quality/quantity. For instance, Gosling and others (1995) concluded that while chipping was labor intensive it nonetheless yielded the fastest germination rate over the widest range of temperatures tested

Table 4

Some Comparative Studies of Different Scarification Methods Applied to Tropical Tree Seeds

Species	Treatment conditions	Comment/response	Reference
Acacia auriculiformis	Nicking, H_2SO_4 15 or 30	Higher germination with	Marunda 1990
A. holosericea	min, hot water 1-5 min	nicking but seedling growth	
		poorer than with other	
		treatments.	
A. farnesiana	Sandpaper scarification:	98% germination	Gill and others 1986
	HNO_3 or H_2SO_4:	65-66% germination	
	Soaking and drying:	64% germination	
	Control, untreated:	30-40% germination.	
A. tortilis,	None (control).	All treatments gave 103-	
A. craspedocarpa,	Mechanical scarification,	186% germination	
A. pachyacra,	hot water treatment,	increase over control;	Omari 1993
A. farnesiana,	mechanical + hot water.	mechanical + hot water	
A. saligna		best overall.	
		Benlate used; 15 °C best.	
Albizzia lebbeck	Hot water 75-100 °C, 3 s +	100% germination	Millat-E-Mustafa 1989
	24 h water soak at room		
	temperature + 24 h high RH		
	hold + direct soil sowing.		
Cassia fistula, C. glauca,	Mechanical, H_2SO_4, and	Mechanical most effective	Todaria and Negim 1992
C. javanica, C. nodosa,	sheep rumen scarification	overall; H_2SO_4 best for C.	
C. sienna	compared.	javanica	
C. bicapsularis, C. javanica,	H_2SO_4 1, 2, 3 h:	54-90% germination	Rodrigus and others 1990
C. speciosa	Boiling water + 8, 12, 24 h		
	soak:	2-12% germination	
	Manual scarification:	69-79% germination	
C. sieberiana	Wide range of heating,		
	organic solvents, mechanical		
	and combinations –		
	Nicking:	93% germination	
	98% H_2SO_4, 45 min:	93% germination	Todd-Bockarie and others
	95% EtoH, 9 h:	40% germination	1993
	Hot or boiling water, 2, 4,		
	6 min:	0-12% germination	
	Commercial mill:	85% germination	
	Control:	2% germination	
	Coffee grinder:	45% germination	
Leucaena leucocephala,	File and sandpaper +	Better response than	Foroughbakhch 1989
L. greggii, Pithecellobium	H_2SO_4 10-20 min	mechanical only	
pallens, P. flexicaulis,			
Propsis laevigata			

Table 4 (continued)

Species	Treatment conditions	Comment/response	Reference
Leucaena leucocephala	95% H_2SO_4, 7 min:	98% germination	
	95% H_2SO_4, 4 min:	99% germination	
	Bag impaction:	64% germination	Passos and others 1988
	Hot water 100 °C, 2 s:	76% germination	(Further details in fig. 4;
	Hot water 100 °C, 4 s:	82% germination	Gosling and others 1995)
	Control:	73% germination	
	H_2SO_4, 1 h:	77% germination	
Terminalia brownii	Control	66% germination	Specht and Shaefer 1990
	V-shaped nick at radicle	81% germination	
	end:		
T. spinosa	No treatment	Weaker endocarp: easy to	
		germinate	
T. ivorensis	H_2SO_4 3 h + cellulase	Most effective treatment for	Corbineau and Côme 1993
	24 h + GA_3 5 d	lignified coat	

for *Leucaena leucocephala.* Hot or boiling water treatments, although easier to apply in bulk, did compromise germination, especially when conducted at higher temperatures. Figure 4, reproduced from Gosling and others (1995), shows clearly the "narrow island" for optimal dormancy-breaking, and strongly emphasizes the interaction of longer times and higher temperatures in producing a larger "sea" of deleterious seed treatments. Indeed, any heat treatment should be regarded as a form of accelerated aging, no matter how short the duration.

Stratification

This is a simple, inexpensive, and effective technique for overcoming seed dormancy of temperate tree species depending upon the type of dormancy involved: warm stratification is applied for seeds that have immature embryos; cold stratification is used to break physiological dormancy; and a combined warm and cold stratification is effective for seeds that have both immature embryos and physiological dormancy. Warm stratification involves placing seeds in a moist medium such as sand, sawdust, vermiculite, peatmoss, or a mixture of two media in a loosely covered container at 20 to 25 °C for various periods of time depending on the species. In the Tropics, warm stratification is not commonly used for releasing dormancy of the tropical tree species although Msanga (1998) has suggested this treatment for *Warbugia salutaris,* which is suspected of having an embryo dormancy with delayed germination.

Cold Stratification

Also known as moist chilling, this involves placing seeds in a moist medium of sand, sawdust, peatmoss, vermiculite, or any other porous material in a loosely covered container (e.g. plastic bag) at 1 to 5 °C for various periods depending on the species. The most commonly practiced method of cold stratification in North America is so-called "naked stratification" which requires soaking seeds in tap water for 24 to 48 hours, draining the water, surface-drying the seeds, and placing them in a loosely tied plastic bag at 2 to 5 °C for various periods. Recently, the cold stratification treatment was modified by drying back the seed moisture content to 10 to 15 percent lower after soaking (i.e. *Abies*) (Edwards 1989, Leadem 1989, Tanaka and Edwards 1986), or surface-drying the seeds in the midstratification period then continuing the stratification period (Tanaka and Edwards 1986). Albrecht (1993) found that seed dormancy of *Juniperus procera* was effectively broken by moist chilling in sand at 3 °C for 60 days. It is interesting to note that seeds of many subtropical orthodox as well as recalcitrant species exhibit deep dormancy and require cold stratification to enhance seed germination (e.g. *Phellodendron wilsonii, Sassafras randaiense, Castanopsis carlesii, Quercus gilva, Quercus glauca, Quercus spinosa, Elaeocarpus japonica, Neolitsea ariabillima,* and *Neolitsea parvigemma*) (Lin and oth-

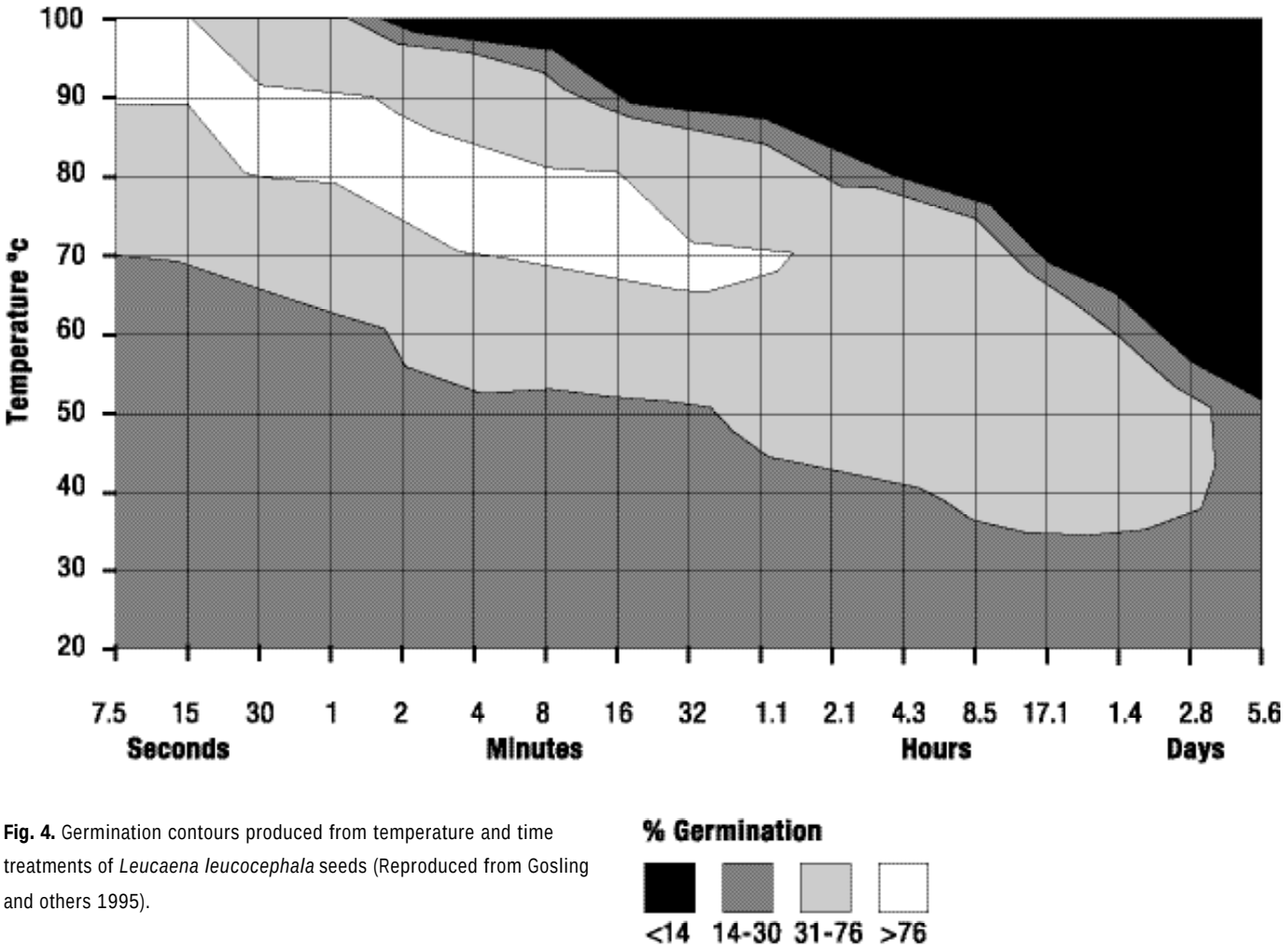

Fig. 4. Germination contours produced from temperature and time treatments of *Leucaena leucocephala* seeds (Reproduced from Gosling and others 1995).

ers 1994, Lin 1994). Chien and others (1998) reported that *Taxus mairei* seeds require not only 6 months of warm stratification at alternating temperatures of 25 °/15 °C or 23 °/11 °C, but also 3 months of cold stratification at 5 °C to overcome the combined morphological and physiological dormancy. Apparently, the warm stratification caused the underdeveloped embryo and ABA concentration to decline, whereas the cold stratification induced the accumulation of GAs and/or increased the sensitivity of seeds to GA's, thus resulting in the release of physiological dormancy and enhancing seed germination (Chien and others 1998). It should be realized that the beneficial effects of cold stratification are not limited to breaking seed dormancy and promoting the percentage and rate of germination; it also minimizes the effects of seed handling and adverse germination environments (Wang 1987).

Chilling for 56 days was recommended for seeds of *Celtis africana, C. sinensis,* and *Pteroceltis tartarinowii* (Browse 1990). In Cuba, seeds of *Quercus oleoides* subsp. *sagraena* responded well to chilling at 4 °C in moist sand at 20 percent moisture content (mc), and 60 percent germination was recorded after 7 months (Figueroa and others 1989). Obviously in species that are known to be recalcitrant, or where ecotypes may exist, the chilling injury limit should be avoided. For instance, Mori and others (1990b) showed that temperatures below 15 °C were deleterious to four species of Malaysian dipterocarp, *Bombax valetonii,* and *Acacia auriculiformis*.

GERMINATION CONDITIONS

Several conditions need to be fulfilled to ensure germination; these include moisture, temperature, aeration (oxygen), light, and an appropriate medium (or substrate), plus a suitable container.

Moisture

The requirement for water as a medium for biochemical processes leading to germination, such as weakening the seedcoat, activating enzymes, and breaking down food reserves, scarcely requires emphasis. It is generally recognized that seed

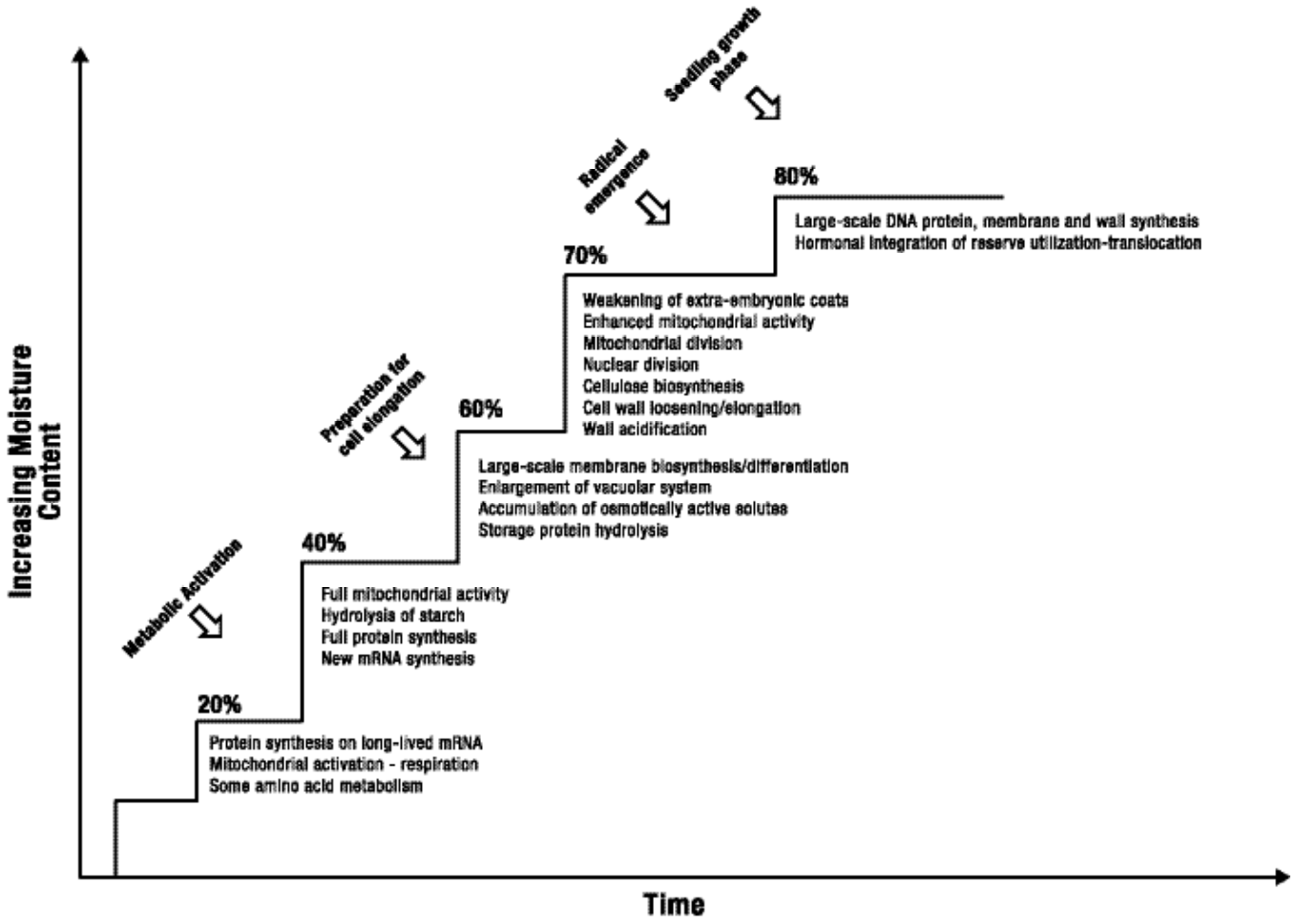

Fig. 5. Some proposed relationships between the major biochemical/structural events and increases in seed water content, which lead to germination and seedling establishment (Adapted from Obroucheva and Antipova 1997). In this model, loss of coat impermeability is associated with hard-coated legumes; nuclear division and cell wall elongation may be synchronous, and precede radicle emergence, or separated in time by the process of radicle emergence. The lack of "milestone" molecular events is a reflection of a paucity of knowledge, rather than a deliberate omission.

germination is more sensitive to moisture stress than is subsequent seedling development (Mayer and Poljakoff-Mayber 1989). In normal germination, the germination medium is sufficiently moistened throughout the course of germination. While inadequate moisture in the medium will result in delayed and poor germination, excessive moisture will hinder germination due to decreased aeration. It is therefore important that the germination medium be not so wet that a film of water forms around the seeds, or, when pressing the medium, a film of water forms on the finger (Bonner and others 1974). Seeds of some tropical species such as *Paraserianthes falcataria* were found to be sensitive to excessive medium moisture in germination (Wang and Nurhasybi 1993).

Some steps associated with water uptake are illustrated graphically in figure 5 and show, in a generalized way, some metabolic and other events which take place at particular hydration levels. It shows four stages associated with the germination process: (1) metabolic activation, (2) preparation for cell elongation, (3) radicle emergence, and (4) seedling growth (Obroucheva and Antipova 1997). A critical event is the requirement for the embryo to overcome the resistance of encompassing tissues. This is achieved by embryos lowering their water potential, by lowering either the osmotic potential or their turgor. That the concept of seed water potential is a crucial event in germination has now been embodied in a model using the concept of hydrotime (Bradford 1996). While not necessarily explaining what germination is biochemically, this model reveals underlying patterns and simple relationships that result in the germination time courses observed for seeds under given conditions. More detailed biochemical aspects of respiratory events, in dormancy and germination, may be found in Côme and Corbineau (1989) and Botha and

others (1992), which are beyond the scope of the present chapter. Although the latter are concerned with cultivated crops it would seem reasonable to assume that some of the patterns seen, say, in cultivated legumes such as peas and beans, share much in common with their arborescent tropical relatives.

The relationship between water and germination (seed survival) for three Panamanian species of the Rubiaceae is illustrated in figure 6 (adapted from Garwood 1986). Seven watering trials were employed, during which buried seeds were watered over a 4-month period by: watering daily for a month; four combinations of not watering for 1 or 2 months; and watering only for 3 days on each of four successive months. Thereafter, all treatments were watered daily for a further 5 months and germination evaluated. What is clear from these results is that species (c) shows a requirement for at least 3 successive months of water availability during early planting (histograms 3 and 5). An extended absence, or intermittent pattern, of water availability for 4 months is essentially lethal (histograms 6 and 7). On the other hand, while species (b) shows some sensitivity in response to an absence of water in the first and third months (histogram 5), withholding water for 4 successive months was not as damaging (histogram 6); this was clearly so for species (a). Although species (a) was not greatly affected by an intermittent water supply over 4 months (histogram 7), species (b) showed only a marginal improvement over the previous treatment. Thus, species (a) appears capable of slowed development (underdeveloped embryo?)

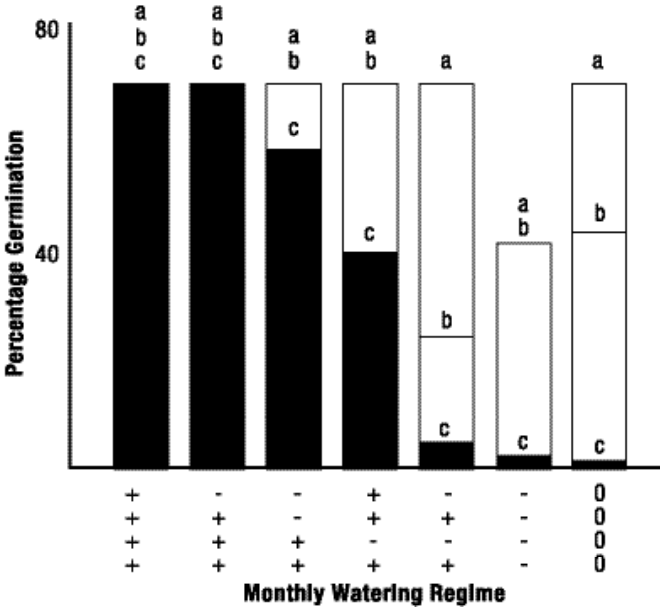

Fig. 6. Relationship between watering regimes and seed survival for three rubiaceous species a, b, and c. += watering daily; -=watering for three days only of each month; 0=no watering for each month (Adapted from Garwood 1989).

when water is limited, whereas species (b) cannot adjust greatly and in (c) there is no adjustment at all. This illustration is used to indicate that while species (a), (b), and (c) "climb the steps" to germination as indicated in figure 4, their requirements for moisture may differ greatly over time with the possibility of "pausing" at certain steps along the progression. Recalcitrant seeds, on the other hand, show little potential for "pausing" and none for reversal of the steps, being "committed" to a continuous water content increase, and germination. Metabolic events associated with recalcitrant seeds were discussed by Berjak and Pammenter in chapter 4. The observation that a 10-percent increase in water content by the excised embryonic axes of dormant seeds was sufficient to ensure germination, and that there are differential patterns of water localization between dormant and nondormant seeds (Hou and others 1997), serves to further stress the importance of water to the germination process. Some further details on water availability, oxygen supply, and synchronization of germination may be found in the upcoming section on oxygen.

Temperature

Because temperature influences both the percentage and rate of germination of seeds, it is one of the most critical factors affecting seed germination. Although seeds of each species have optimal temperatures for attaining maximum germination, most species can reach their maximum germination at an alternating temperature regime of an 8-hour day at 30 °C with light and a 16-hour night in darkness at 20 °C (AOSA 1992, International Seed Testing Association 1996). Alternating temperatures are preferred to constant temperatures because they can overcome shallow seed dormancy and enhance uniform germination. Some of the subtropical tree seeds like *Taxus mairei* and *Cinnamomum camphora* require an alternating temperature regime for releasing dormancy as well as for germination (Chien and Lin 1996, Chien 1997). When alternating temperatures of 30 °/20 °C, which are prescribed for most tree seed germination (AOSA 1992, International Seed Testing Association 1996), are not available, a constant temperature of 25 °C can substitute for them. For most tropical tree seeds, room temperature of 25 to 30 °C in the Tropics will be quite suitable for maximum germination. The temperature effect can be modified by light as well as by moist chilling treatment (Wang 1987).

Liengsiri and Hellum (1988) noted that while six different provenances of *Pterocarpus macrocarpus* showed different germination characteristics, maximum final germination could be attained for all sources using alternating temperatures of 30 °/25 °C (8:16 hr). Corbineau and Côme (1986) reported that the optimal temperature for the germination of the recalcitrant

species *Shorea roxburghii* and *Hopea odorata* was 30 to 35 °C. Differences were also noted between the lower temperature limits for seed germination in the two species, and these were different from those of seedlings.

When the germination of isolated embryos of seven species of *Inga* was investigated by Pritchard and others (1995), it was found that radicle elongation was possible at temperatures of 11 °C, but no epicotyls were produced. This further supports the idea that radicle emergence may not accurately reflect the ability of the embryo to produce a seedling.

Optimum germination temperatures for *Prosopsis argentina* and *P. alpataco* were shown to be 35 °C, with the minimum temperature being 15 °C and the maximum 40 °C (Villagra 1995); other studies have indicated somewhat lower temperature optima (e.g. 25 °C for *P. flexuosa* and *P. chilensis*) although the lower temperature limit of 15 °C seems to be common throughout (Catalan 1992). Seeds of *Ochroma lagopus* are stimulated by very high temperatures, possibly attributed to an association with fire in the natural habitat. The presence of a suberized light line in the palisade cells of the sclerenchymatous seedcoat, suggested parallels with the coat-imposed dormancy of legumes (Vazquez-Yanes and Orozco-Segovia 1993).

Seed germination and seedling growth were investigated for several Malaysian species by Mori and others (1990b), including *Shorea assamica, S. parviflora, Dryobalanops aromatica, Neobalanocarpus heimii, Bombax valetonii, Duabanga grandiflora,* and the exotic *Acacia auriculiformis.* Not surprisingly, performance was linked to the day/night temperature regimes of their respective ecotypes.

Seeds of *Manihot glaziovii* are known to be deeply dormant, possibly as a result of coat-imposed dormancy. Drennan and Van Staden (1992) found that, while incubation of seeds at 25 °C gave 70 percent germination after 14 days, temperatures of 35 °C resulted in 98 percent germination, but only if seeds were subjected to a temperature shift to 25 °C after 21 days. Exposure to the ethylene-producing compound, ethrel, resulted in over 90 percent germination within 14 days, over the temperature range 20 to 30 °C. Temperatures of 35 °C and 40 °C were inhibitory to germination and, unless seeds were subjected to a temperature shift, no improvement in germination was seen in the presence of ethrel.

Oxygen

Seeds of many species will not germinate well at an oxygen level considerably lower than that normally present in the atmosphere (Mayer and Poljakoff-Mayber 1989). In laboratory germination tests, seeds of most tree species germinate well with the air available in the germination medium and with exchange through loosely fitting germination containers. Germination will be inhibited by depressed oxygen supply when there is excessive moisture in the medium. As a general rule, oxygen availability should not be a concern in the Tropics since germination usually takes place in the open at room temperatures.

While the above generalizations may be entirely appropriate for most tropical tree species, the situation may be quite different for some seeds of the flood plain forests of Amazonia. Kubitzki and Ziburski (1994) have noted that (under field conditions) *Swartzia polyphylla* seeds are dispersed after peak inundation and germination begins almost immediately (b, in fig. 8), whereas in *Pithecellobium inaequale* fruiting occurs between May and June, coincident with near-peak flooding (*Pithecellobium* and *Pachira* were regarded as showing precocious germination), and germination commenced within 2 months. Interestingly, *Pithecellobium adiantifolium* shows a more "failsafe" strategy; germination starts after the majority of forest species had already begun germinating (third horizontal line from bottom of fig. 8 representing fruiting duration, and the dot at S indicating start of germination). By way of contrast, *Laetia corymbulosa* and *Simaba orinocensis* have peak fruiting early in the inundation cycle (third horizontal line from top of fig. 8) and "mark time" for some 5 months until commencement of germination. *Pseudobombax munguba* was identified as an obligate light-requiring species with minimal time between fruiting, dispersal, and germination (second from bottom, fig. 8). *Triplaris weigeltiana* showed an extremely compressed and "tail-end" synchronization (c, in fig. 8). Germination was nonetheless rapid, within 2 months of peak

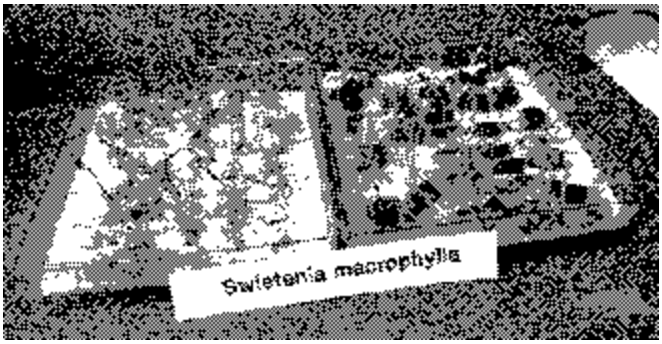

Fig. 7a.

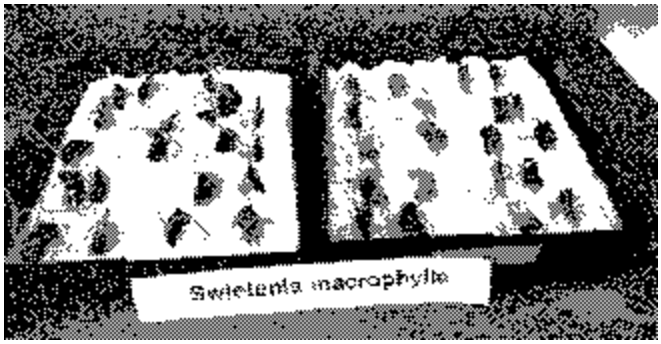

Fig. 7b.

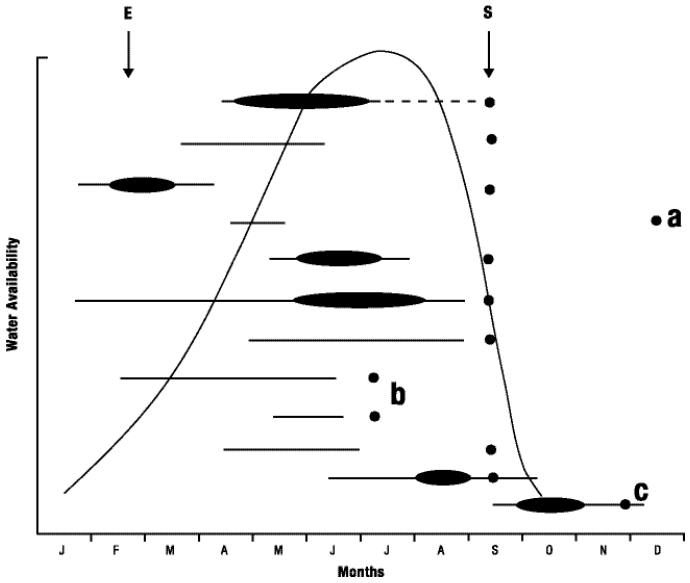

Fig. 8. Illustrates relationship between water availability on Amazonian floodplain (bell-shaped curve) and duration of fruiting period for several tree species. In some, peak fruiting is illustrated by the dilated parts on the horizontal lines. Although these are temporally very diverse (duration and length), the start of germination is mostly synchronoous at (•); the start and end of germination are indicated by the arrows at S and E. See text for further details (Adapted from Kubitski and Ziburski 1994).

fruiting. This latter species appears to be a standard, orthodox species with a wind-dispersed fruit and no dormancy mechanism. What is perhaps most striking about the information presented in figure 8 is the predominant initiation of germination in August-September of 85 percent of the 33 species studied; only 15 percent were outliers (as represented by species a, b, and c). This synchronous start to germination occurred irrespective of the duration of the fruiting period. What mechanism can act to produce such a remarkable synchrony? Kubitzki and Ziburski (1994) suggest that for many species the low oxygen tensions associated with immersion provide a dormancy-breaking cue. Strong experimental support for such a proposal was obtained for *Simaba orinocensis*, *Pouteria cuprea*, and some other species; only 30 percent of species studied showed no positive response to annoxia. It is important to realize that while the germination data given above do not all represent tree species, they strongly suggest that germination cues used by some tropical trees may well differ to a significant degree from those used by domesticated crops.

Light

Light is an important factor for seed germination, with both positive and negative effects. The promotional effect of light is through a single photoreaction controlled by the blue pigment phytochrome. The phytochrome is known to exist in two photoconvertible forms: P_2, which absorbs light @ 660 nm; and P_{fr}, the far red light which absorbs light @ 730 nm. Seeds of many temperate tree species are known to be light sensitive, and their germination is promoted by red light and inhibited by far red light (Toole 1973). For light to be effective, seed moisture has to reach a threshold level. For North American jack pine (*Pinus banksiana*) seeds, the threshold moisture content is 17 percent of fresh weight (Ackerman and Farrar 1965). The effectiveness of light on germination is temperature dependent (Ackerman and Farrar 1965) and interacts with moist chilling treatment (Pons 1992). Unfortunately, there is little information on the requirement of light for optimum germination of tropical tree seeds. Judging from their natural habitats, seeds of some species in the Tropics may require little or no light for germination. Therefore, daylight should meet the requirement for tropical seed germination. Surprisingly, it was found in one case that the *Swietenia macrophylla* seeds germinated well, without fungal infection, in the dark, in comparison to those germinated under light (fig. 7) (Wang and Nurhasybi 1993). No obvious explanation is available for these results.

It is generally held that the requirement for light (quantitative and qualitative) is associated with smaller seeds and dormancy mechanisms. Germination is triggered by increases in light as well as by the ratio of red to far-red light and temperature (Denslow 1987). Except for the well-documented case of *Cecropia obtusifolia,* evidence for classical red light responses are lacking (Vazquez-Yanes and Smith 1982). The light requirements for four species of *Cecropia* from the Amazonian flood plains were investigated by Kubitzki and Ziburski (1994). Two showed no obligate requirements for light, and germinated equally well in darkness (*C. latiloba, C. membranacea*) whereas *C. concolor* was unable to germinate in the dark, and *C. ulei* germinated poorly (17 percent) in the light. Significantly, the latter two species were typically associated with drier, noninundated habitats. Molofsky and Augspurger (1992) have provided evidence from field studies that the small-seeded *Luehea seemanni* is strongly light requiring, whereas the large-seeded *Gustavia superba* showed a minimal light requirement for germination.

Perhaps until more precise information on the light responses of tropical trees is forthcoming, it may be more appropriate to adopt the four categories recognized by Schultz (1960). The first were light-requiring, short-lived species such as *Cecropia*; the second, longer-lived, strongly light-demanding "nomads" such as *Simarouba amara,* which gives 60 to 80 percent germination in full light; the third, those which germinate better in light than in darkness such as *Jacaranda copaia*; and finally a large group of primary forest species which germinate naturally under closed forest canopies or maybe even in dark-

ness (during later development, however, light requirements may be evident). It may seem reasonable to assume that the category "prompt germinators," frequently used to describe seeds of tropical tree species, may well reflect an absence of light (and perhaps other particular) requirements. Vazquez-Yanes and Orozco-Segovia (1984) cite studies by several other authors from different tropical forests of the world which show a high incidence of rapid germinators: 65 percent of the woody flora of Malaysian forests, 79 percent of species studied in the Ivory Coast, and 9 out of 10 species examined in Zaire.

Light-regulated germination is commonly reported in many ecological studies in relation to primary tree species, secondary invaders, and weedy species for tropical forests. *Macaranga, Musanga, Trema, Melastoma,* and *Maclura* seem to fall into this generalist category (Bazzaz and Pickett 1980). Light-temperature interactions also exist, but evidence is available only for *Schefflera* and *Ochroma* (Vazquez-Yanes and Orozco-Segovia 1984). The paucity of knowledge in this area probably reflects the fact that the majority of tropical tree species may show only minimal light requirements (their generally larger seed size may militate against this also), as well as the fact that the "rapid" germination strategy appears to minimize its importance; this does not mean that quite exquisite, qualitative and quantitative mechanisms await discovery.

For example, Drake (1993a) has shown that for *Metrosideros polymorpha* germination was greater under white, red, or far-red light (all $\leq$62 percent) compared to dark treatments. The light requirement could not be overcome by fluctuating temperature treatments (5/15 °C or 15/25 °C). Far-red responses of seeds of *M. polymorpha* var *polymorpha* were greater than those of *M. polymorpha* var *macrophylla*, which differ primarily in having pubescent and glabrous leaves.

Germination Media (Substrates)

The media generally used for germination are sand and/or soil. However, for seed germination testing, filter papers, blotters, agar, or sand are recommended (AOSA 1992, ISTA 1996). Each germination medium has its own property and suitability for different species. In the Tropics the cost and availability of certain media are also important factors. In the National Tree Seed Centre of Petawawa National Forestry Institute, Chalk River, ON, Canada, Kimpak (cellulose cotton) was commonly used for germination tests of most tree species, but it has become expensive and difficult to procure in recent years. A wide range of seed germination papers are available from Anchor Paper Company, St. Paul, MN, U.S.A. (Internet site: www.anchorpaper.com). In the Tropics, paper towels and sand are used for small and large seed germination tests, respectively, in the ASEAN Forest Tree Seed Centre, Thailand. Sand is the standard germination medium used for germination tests of all species in the National Tree Seed Program in Tanzania (Msanga 1998). Sand is probably the most suitable medium for tropical tree seed germination due to its availability, low cost, capacity to hold moisture, and suitability for large seeds.

Media should not only be adapted to suit availability under local conditions, but the approach of "one substrate suits all" should be cautioned against. For example, with recalcitrant seeds of *Podocarpus milanjianus*, Schaefer (1990) compared the effects of cold storage in perforated polyethylene bags without medium against those of damp sawdust or peat. Although the exact extent of hydration of the latter media was not recorded, seeds in peat lost moisture compared with those kept in polyethylene bags (ca. 43 percent m.c.), while sawdust-stored seeds increased to 58 percent m.c., and gave 72 percent germination.

Over the last few years evidence has been accumulating to suggest that the germination medium has importance beyond merely being a medium for water retention and transmission of light. When the seeds of eight weedy species were placed on the surface of an agar substrate, or 2 mm below the surface, in a variety of orientations, some surprising results were observed. Five of the eight species showed less germination when planted with radicle ends pointing downward, two showed no differential response to orientation, while one species responded poorly to burial and germinated best when on the agar surface (Bosy and Aarssen 1995). These authors speculated that uneven exposure to gravity, oxygen, or light may have been responsible for these effects. No significant effect of different soil types (loamy soil; washed, sterile river sand; or nonsterile river sand) was seen on the emergence of *Ceiba pentandra, Leucaena leucocephala, Gmelina arborea,* and *Tectona grandis*, although *T. grandis* germination was orientation sensitive (Agboola and others 1993). Seeds of *Bauhinia retusa* germinated best if sown with the radicle end upward, while performance was poorest if the radicle end was directed downward (Prasad and Nautiyal 1995). These authors interpreted the greater success of the root-upward orientation to the fact that as soon as the radicle emerges, it turns downward under the influence of geotropism, thereby facilitating a "hook" for easier shoot emergence.

Where seeds are very small, e.g. *Metrosideros polymorpha* (seed mass ca. 57µg), depth of burial can have serious impact on germination. Seedling emergence for seeds buried at a depth of 2 mm in sand was half that of surface-sown seed and minimal at 5 mm depths; 6 to 10 percent germination was recorded in continuous darkness (Drake 1993a).

GERMINATION BOXES OR TRAYS

There are no specifications for germination boxes and trays

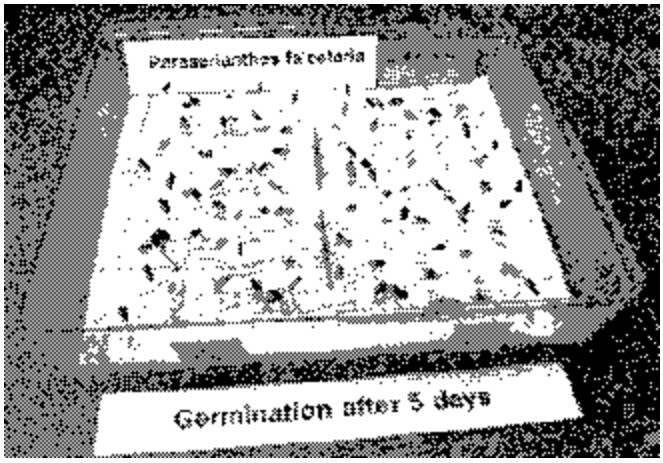

Fig. 9-1.

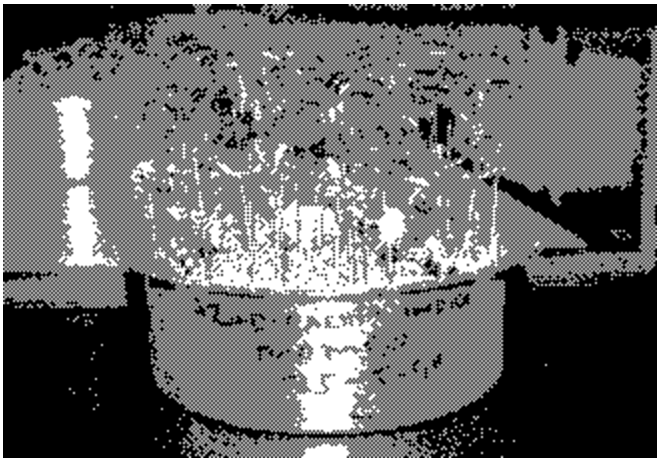

Fig. 9-2.

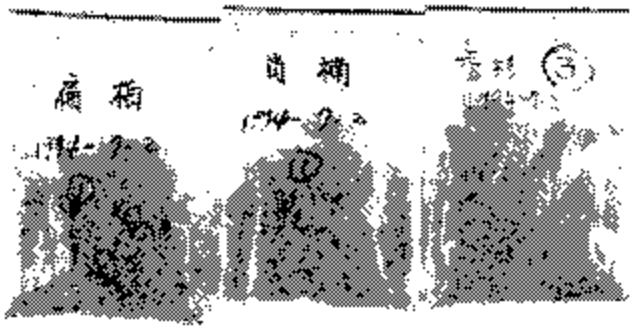

Fig. 9-3A.

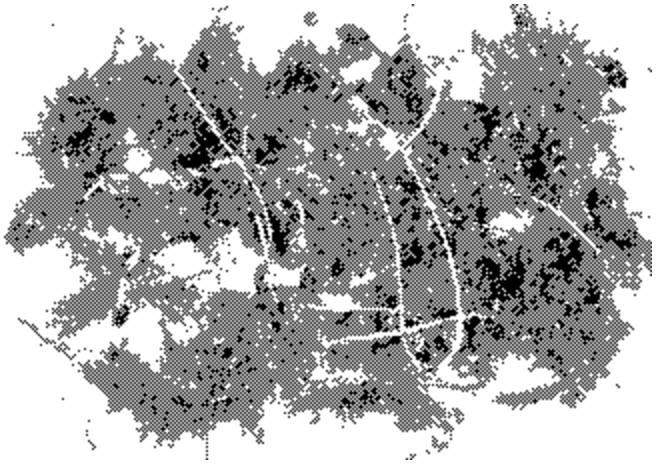

Fig. 9-3B.

for standard germination tests in the international rules for seed testing. Petri dishes or plastic boxes of various sizes are commonly used for germination tests or research on tree seeds. However, these boxes and dishes are usually too small for proper tropical tree seed germination tests and often promote a serious fungal growth problem. The lids of some of the boxes may be too tightly fitting and suppress air circulation. More recently, a specially designed germination box has been tested and considered ideal for germination tests or research (Wang and Ackerman 1983). The germination boxes are commercially available and widely used in many countries of the world (fig. 9-1). In Tanzania, an aluminum bowl is used in conjunction with washed river sand as a medium for germination tests (Msanga 1998) (fig. 9-2). For tropical seed germination, it is important that the capacity of the germination box or tray be large enough to avoid crowding and fungal contamination.

In the Seed Laboratory of Taiwan Forestry Research Institute, sealable polyethylene bags are used with sphagnum medium for all seed germination tests and research (Chien and Lin 1996, Chien and others 1998) (figs. 9-3A and 9-3B).

ASSESSMENT OF GERMINATION

Although there are many indirect, rapid tests for evaluating seed quality, they are not always reliable for assessing seed viability. For evaluating the germinability of seeds, the only dependable technique is the direct growth method or germination tests. The laboratory standard germination tests for seeds of tree species in international trade have been well described and documented (AOSA 1992, International Seed Testing Association 1996). Unfortunately, such well-established germination test protocols are not available for tropical tree seeds, although those rules are often applied for tropical tree seed germination and germination testing. Because of the nature of tropical tree seeds, there have been some research attempts to establish standards for tropical tree seed germina-

tion tests. Williams and others (1992) recommended four 25-seed replications for *Acacia* seed germination tests and compared the maximum tolerated range of variation with the ISTA prescription of four 100-seed replications. The authors also recommended a reduction in the number of seeds used for large-seed germination tests due to the amount of space required for such large seeds as *Syzygium suborbiculare* and *Castanopspermum australe.*

In Malaysia, Krishnapillay and others (1991) established a test standard for determining the moisture content for *Hopea odorata* seeds. They suggest that a sample size of 20 to 25 seeds would be sufficient for accurate seed moisture content determination where the seeds can be oven-dried at either 103 °C for 20 hours of 90 °C for 24 hours.

Our understanding of tropical tree seeds has advanced considerably over the last 20 years, and is perhaps moving from a stage of collection of information to one of consolidation and more goal-directed work on specific physiology. However, as Bewley (1997) has noted, we still cannot answer the two fundamental questions: how does the embryo emerge from the seed and how is emergence blocked in dormancy? Evidence is now accumulating from the cultivated crop species to suggest that ABA prevents radicle extension and maintains dormancy, whereas GA's seem to be involved in the promotion and maintenance of germination after ABA-mediated events are overcome. For tropical tree species such basic information is lacking, in spite of the greater ease and sophistication of the analytical techniques available. Geographical distance and lack of funding are partly to blame for this anomaly, as is perhaps the fact that seed physiology and biochemistry can more safely (and profitably, because of funding) be conducted on cultivated crops.

While the above goals may be seen to have highlighted the shortcomings of short-term research, the prospects for the longer-term activities appear much brighter. International symposia on genetic conservation and the production of tropical tree seed provide proof that there is much to be proud of, although it admittedly is heavily biased in favor of *Acacia, Casuarina,* and *Eucalyptus* spp. Some of the noteworthy publications in this regard are by Arisman and Havmoller (1994), Boland (1989), Harwood and others (1991), Midgley (1990), and Thomson and Cole (1987).

Breeding programs, recurrent selection, along with identification of genetic diversity and its maintenance, are receiving increasing attention, even if the rewards appear to be long term (Bangarwa and others 1995, Bumatay and others 1994, Chamberlain and Galwey 1993, Harwood 1990, Harwood and others 1994, Namkoong and others 1988, Plumptre 1995, Singh and Deori 1988, Wood 1976).

A greater awareness now exists of the effects of afforestation by "alien" species on stream flows, and the long-term nature of recovery to preplantation levels (Scott and Lesch 1997); attempts at the restoration of degraded natural forests (Alexander and others 1992, Ray and Brown 1995) strongly underscore the role of seed optimization and seedling establishment in the process. The role of rhizobia, vesicular-arbuscular mycorrhizal fungi, nodulation by the actinomycete *Frankia*, as well as suitable phosphate or liming applications are now recognized as important elements of seedling growth. In this regard some valuable studies have emerged for *Albizia, Casuarina, Parkia, Dalbergia, Enterolobium, Gliricidia, Intsia, Leucaena, Sesbania,* and *Shorea* (Diem 1996, Dommergues 1996, Lang and others 1995, Osundina 1998, Sayed and others 1997, Surange and others 1997).

Tropical tree seeds will continue to provide mankind with much-needed resources only if researchers remain challenged by the need to understand the many aspects of seed biology, and if governments and international agencies continue to provide the necessary funding and platforms for research, collaboration, and international exchange. The world's 2950 million hectares of forest will shrink further if economic gain is allowed to override sound management practices.