

# THE ECOLOGY AND PHYSIOLOGY OF VIVIPAROUS AND RECALCITRANT SEEDS

---

Elizabeth Farnsworth

*Smith College, Clark Science Center, Northampton, Massachusetts 01063;  
e-mail; efarnswo@mtholyoke.edu*

**Key Words** desiccation intolerance, dormancy, plant reproduction, phytohormones

■ **Abstract** Understanding seed physiology is central to reconstructing how angiosperms have evolved, to characterizing dormancy and germination regimes shared by suites of species, and to devising sound strategies for seed bank conservation, agriculture, and forestry. While species with dormant seeds have received the lion's share of attention, hundreds of plant species exhibit no seed dormancy and germinate either viviparously on the parent plant or shortly after release. Embryos of these recalcitrant and viviparous species cannot tolerate the maturation drying that is usually prerequisite to dormancy; such desiccation intolerance creates challenges for storing and preserving such embryos. I review the physiology, morphology, and ecology of these desiccation-intolerant, nondormant lineages. Differences in the production and function of plant hormones are implicated in the occurrence of recalcitrance and vivipary in plant families. Plant hormones are key regulators of seed physiology and simultaneously coordinate responses of the seedling and mature plant to their environment. Desiccation-intolerant embryos occur most commonly among species of wet or flooded environments and have evolved multiple times in disparate lineages. Natural selection in wetland environments simply may not eliminate these seed types or may select for changes in hormone physiology that simultaneously affect both maternal and embryonic tissues. Integrative data from ecological, genetic, and physiological studies are needed to elucidate evolutionary origins and maintenance of reproductive strategies in organisms.

## A COMPARATIVE STUDY OF SEED PHYSIOLOGY

Most species exhibit a critical capacity to control the timing of their reproduction and the establishment of a new generation of offspring. Seeds, cysts, planktonic larvae, and other mobile propagules—hardy and compact phases in the life history of many taxa—enable organisms to disperse in space and to persist in time. Many of these forms exhibit some type of dormancy or metabolic quiescence involving a delay between fertilization and subsequent establishment. Dormancy and other complex life history traits are under physiological control, which, in turn,

is regulated through mechanisms of gene action that are now being elucidated through intensive study. In particular, comparative and experimental studies of the activity and evolution of the ubiquitous and powerful hormones that mediate responses of both embryos and mature organisms to their environment can help illuminate many aspects of life history.

I consider the case of angiosperm seed physiology as a model system for investigating the hormonal control of traits in general. I review the physiological, morphological, and ecological characteristics shared by 195 plant species that exhibit no dormancy (Table 1) and hypothesize—on the basis of evidence from these as well as other species that precociously germinate or exhibit hormonal mutations—that they share consistent features of hormonal physiology. These species are common to predominantly wet or flooded environments, indicating that these habitats select for (or do not select against) these types of hormonal pathways. I posit that integrative data from ecological, genetic, and physiological studies are needed to elucidate evolutionary origins and adaptive costs and benefits of reproductive strategies in organisms.

## DEFINING STATES OF SEEDS: Dormancy, Vivipary, and Recalcitrance

This review focuses on two types of nondormant seeds: those that are viviparous and those that are recalcitrant. Plant species in which the embryo grows sufficiently to emerge visibly from within the seed tissues *before* dispersal are termed viviparous (42, 68, 173). Vivipary (cf “viviparity,” a term used by zoologists) is a relatively rare form of plant reproduction among angiosperms, but has been remarked upon by botanists for centuries (Table 1). In some plant species, the viviparous embryo can attain prodigious sizes and can grow for several months prior to release. Truly viviparous plants should not be conflated with species that produce apomictic or asexual plantlets or bulbils instead of embryos derived from sexual fertilization, although many of these latter taxa bear the species name *viviparum* (42, 68, 181). A precise definition of vivipary implies that formation of a seed and growth of the sexually generated embryo are integral to the process. Thus, vivipary can be studied and compared with germination processes in the context of seed development, physiology, and dispersal.

In another set of species (Table 1), the embryo sustains metabolic activity throughout ontogeny but bursts the seed tissues shortly after dispersal. In natural populations, these seeds may germinate readily within the fruit or soon after dehiscence, and they do not persist in the soil seed bank. These types of embryos rapidly lose viability if they are dried or chilled; hence they are termed “recalcitrant” to storage (146). The term recalcitrant is generally applied to seeds that have been systematically tested to determine their ability to tolerate desiccation (40). The inability to store seeds of these species creates challenges

**TABLE 1** Plant species with recalcitrant or viviparous seeds<sup>a</sup>

Family	Species	Life form	Latitude	Habitat	Seed status	Source
Aceraceae	<i>Acer</i> spp. (3)	T	T	Mesic forest	R	82
Alismataceae	<i>Sagittaria latifolia</i>	H	T	Wetland	R	124
Anacardiaceae	<i>Mangifera indica</i>	T	TR	Wet forest	R	28
Annonaceae	<i>Cymbopetalum baillonii</i>	ST	TR	Wet forest	R	142
Apocynaceae	<i>Hancornia speciosa</i>	T	TR	Wet forest	R	128
Apocynaceae	<i>Landolphia kirkii</i>	V	TR	Wet forest	R	12
Araceae	<i>Dieffenbachia longispatha</i>	S	TR	Wet forest	V	86
Araceae	<i>Xanthosoma sagittifolium</i>	S	TR	Swamp forest	R	42
Araliaceae	<i>Hedera helix</i>	V	T	Mesic cultivar	R	71
Araucariaceae	<i>Agathis robusta</i>	T	TR	Wet forest	R	201
Araucariaceae	<i>Araucaria</i> spp. (2)	T	TR	Coast	R	201
Arecaceae	<i>Areca catheca</i>	P	TR	Wet forest	R	28
Arecaceae	<i>Calamus</i> spp. (2)	P	TR	Swamp forest	R	115, 122
Arecaceae	<i>Chrysalidocarpus leutecens</i>	P	TR	Wet forest	R	11
Arecaceae	<i>Cocos nucifera</i>	P	TR	Coast	V	28
Arecaceae	<i>Elaeis guineensis</i>	P	TR	Wet forest (ag.)	R	28
Arecaceae	<i>Nypa fruticans</i>	P	TR	Coast	V	173
Arecaceae	<i>Sabal</i> spp. (2)	P	TR	Wet forest (ag.)	R	28
Asteraceae	<i>Abrotanella linearis</i>	S	ST	Wet forest	V	22
Asteraceae	<i>Acamptopappus</i> sp.	S	ST	Desert	R	201
Asteraceae	<i>Pachystegia insignis</i>	S	ST	Wet forest	V	22
Avicenniaceae	<i>Avicennia</i> spp. (8)	T	TR	Coast	V	53
Bombacaceae	<i>Durio zibethinus</i>	T	TR	Wet forest	R	28
Bombacaceae	<i>Montezuma speciosissima</i>	T	TR	Wet forest	V	118
Boraginaceae	<i>Cordia alliodora</i>	T	TR	Wet forest	R	185
Burseraceae	<i>Dacryodes excelsa</i>	T	TR	Wet forest	R	118
Caricaceae	<i>Jacaratia dolichaula</i>	ST	TR	Wet forest	R	86
Caryophyllaceae	<i>Scheidea diffusa</i>	S	TR	Montane	V	10
Celastraceae	<i>Salaciopsis ingifera</i>	V	TR	Wet forest	V	33
Ceratophyllaceae	<i>Ceratophyllum</i> sp.	H	TR	Riverine	R	190
Chenopodiaceae	<i>Chenopodium quinoa</i>	H	T	Agriculture	R	40
Chrysobalanaceae	<i>Coupeia polyandra</i>	ST	TR	Wet forest	R	142
Clusiaceae	<i>Garcinia mangostana</i>	ST	TR	Wet forest (ag.)	R	28
Clusiaceae	<i>Symphonia globulifera</i>	ST	TR	Wet forest	R	185
Combretaceae	<i>Conocarpus erectus</i>	ST	TR	Coast	R	173

(Continued)

TABLE 1 (Continued)

Family	Species	Life form	Latitude	Habitat	Seed status	Source
Combretaceae	<i>Laguncularia racemosa</i>	T	TR	Coast	R	173
Connaraceae	<i>Connarus grandis</i>	ST	TR	Wet forest	V	33
Cornaceae	<i>Corokia macrocarpa</i>	S	ST	Wet forest	V	22
Cornaceae	<i>Griselinia</i> spp. (2)	S	ST	Riverine	V	22
Corylaceae	<i>Corylus americana</i>	ST	T	Mesic forest	R	28
Cucurbitaceae	<i>Sechium edule</i>	H	T	Agriculture	V	28
Cucurbitaceae	<i>Telfaira occidentalis</i>	S	TR	Agriculture	R	40
Cupressaceae	<i>Cupressus macrocarpa</i>	ST	TR	Wet forest	R	2
Cymodoceaceae	<i>Amphibolus</i> spp. (2)	H	TR	Coast	V	38
Cymodoceaceae	<i>Thalassodendron</i> spp. (2)	H	TR	Coast	V	173
Dipterocarpaceae	<i>Anisoptera laevis</i>	T	TR	Wet forest	R	201
Dipterocarpaceae	<i>Dipterocarpus</i> spp. (8)	T	TR	Wet forest	R	126
Dipterocarpaceae	<i>Dryobalanops aromatica</i>	T	TR	Wet forest	R	126
Dipterocarpaceae	<i>Hopea</i> spp. (8)	T	TR	Wet forest	R	126
Dipterocarpaceae	<i>Parashorea densiflora</i>	T	TR	Wet forest	R	126
Dipterocarpaceae	<i>Shorea robusta</i>	T	TR	Wet forest	R	201
Dipterocarpaceae	<i>Stemonoporus oblongifolius</i>	T	TR	Wet forest	R	126
Ebenaceae	<i>Diospyros virginiana</i>	ST	ST	Mesic forest	R	201
Elaeocarpaceae	<i>Sloanea berteriana</i>	T	TR	Wet forest	R	126
Euphorbiaceae	<i>Dalechampia scandens</i>	V	TR	Mesic forest	R	127
Euphorbiaceae	<i>Hevea brasiliensis</i>	T	TR	Wet forest	R	28
Fabaceae	<i>Castanospermum australe</i>	T	TR	Coast	R	190
Fabaceae	<i>Inga</i> spp. (2)	ST	TR	Swamp forest	V	120
Fabaceae	<i>Mora oleifera</i>	T	TR	Coast	V	87
Fabaceae	<i>Pithecellobium racemosum</i>	T	TR	Wet forest	V	105
Fagaceae	<i>Castanea dentata</i>	T	T	Mesic forest	R	28
Fagaceae	<i>Lithocarpus densiflorus</i>	T	T	Mesic forest	R	201
Fagaceae	<i>Quercus</i> spp. (3)	T	T	Mesic forest	R	58
Flacourtiaceae	<i>Casearia corymbosa</i>	T	ST	Wet forest	R	86
Flacourtiaceae	<i>Dovyalis hebecarpa</i>	ST	T	Agriculture	R	28
Flacourtiaceae	<i>Flacourtia indica</i>	ST	TR	Wet forest	R	28
Flacourtiaceae	<i>Muntingia calabura</i>	ST	TR	Wet forest	R	66
Hippocastanaceae	<i>Aesculus hippocastanum</i>	ST	T	Mesic forest	R	175
Lauraceae	<i>Machilus thunbergii</i>	ST	TR	Swamp forest	R	112
Lauraceae	<i>Nectandra ambigens</i>	ST	TR	Wet forest	R	142
Lauraceae	<i>Persea americana</i>	S	ST	Wet forest	R	28
Lecythidaceae	<i>Barringtonia racemosa</i>	T	TR	Coast	V	126

(Continued)

TABLE 1 (Continued)

Family	Species	Life form	Latitude	Habitat	Seed status	Source
Lecythidaceae	<i>Bertholletia excelsa</i>	T	TR	Wet forest	R	86
Lecythidaceae	<i>Lecythis ampla</i>	T	TR	Wet forest	R	86
Liliaceae	<i>Crinum capense</i>	H	TR	Riverine	V	9, 71
Liliaceae	<i>Hymenocallis</i> spp. (2)	H	ST	Riverine	V	42
Liliaceae	<i>Nerine</i> sp.	H	TR	grassland	V	42
Liliaceae	<i>Ripogonum scandens</i>	H	ST	Wet forest	V	23
Lobeliaceae	<i>Lobelia</i> sp.	S	TR	Montane	R	190
Loganiaceae	<i>Fagraea fragrans</i>	S	TR	Wet forest	R	66
Magnoliaceae	<i>Magnolia portoricensis</i>	ST	TR	Wet forest	R	118
Magnoliaceae	<i>Michelia champaca</i>	T	TR	Wet forest	R	28
Melastomataceae	<i>Melastoma malabathricum</i>	S	TR	Swamp forest	R	66
Meliaceae	<i>Aglaia odorata</i>	S	TR	Wet forest	R	201
Meliaceae	<i>Carapa guianensis</i>	T	TR	Swamp forest	R	86
Meliaceae	<i>Guarea glabra</i>	T	TR	Wet forest	R	118
Meliaceae	<i>Turrianthus africana</i>	T	TR	Wet forest	R	185
Moraceae	<i>Artocarpus heterophyllus</i>	T	TR	Wet forest	R	28
Moraceae	<i>Morus latifolia</i>	ST	ST	Wet forest	V	40
Myristicaceae	<i>Myristica holhrungii</i>	T	TR	Swamp forest	V	190
Myrsinaceae	<i>Aegiceras</i> spp. (2)	ST	TR	Coast	V	173
Myrtaceae	<i>Amomyrtus lama</i>	T	ST	Wet forest	R	201
Myrtaceae	<i>Eugenia</i> spp. (2)	ST	TR	Wet forest	R	28
Nepenthaceae	<i>Nepenthes gracilis</i>	E	TR	Swamp forest	R	66
Nyctaginaceae	<i>Pisonia longirostris</i>	T	TR	Swamp forest	V	33
Nymphaceae	<i>Nymphaea</i> sp.	H	TR	Riverine	R	190
Nyssaceae	<i>Nyssa aquatica</i>	T	ST	Swamp forest	R	190
Oxalidaceae	<i>Averrhoa carambola</i>	ST	TR	Wet forest	R	28
Oxalidaceae	<i>Oxalis</i> sp.	S	T	Mesic forest	R	28
Pellicierieaceae	<i>Pelliciera rhizophorae</i>	T	TR	Coast	V	87
Piperaceae	<i>Piper hispidum</i>	S	TR	Wet forest	R	185
Plumbaginaceae	<i>Aegialitis</i> spp. (2)	S	TR	Coast	V	173
Poaceae	<i>Spartina anglica</i>	H	T	Coast	R	140
Poaceae	<i>Zizania aquatica</i>	H	T	Wetland	R	14, 140
Podocarpaceae	<i>Dacrycornus dacrydioides</i>	ST	ST	Mesic forest	R	37
Podocarpaceae	<i>Podocarpus henkelii</i>	S	ST	Mesic forest	R	37
Polygonaceae	<i>Fagopyrum esculentum</i>	H	T	Agriculture	V	40
Potamogetonaceae	<i>Potamogeton</i> sp.	H	T	Wetland	R	124
Proteaceae	<i>Macadamia ternifolia</i>	ST	TR	Agriculture	R	28

(Continued)

TABLE 1 (Continued)

Family	Species	Life form	Latitude	Habitat	Seed status	Source
Ranunculaceae	<i>Caltha palustris</i>	H	T	Wetland	R	190
Rhizophoraceae	<i>Bruguiera</i> spp. (6)	T	TR	Coast	V	173
Rhizophoraceae	<i>Carallia brachiata</i>	ST	TR	Swamp forest	R	201
Rhizophoraceae	<i>Ceriops</i> spp. (3)	ST	TR	Coast	V	173
Rhizophoraceae	<i>Kandelia candel</i>	ST	TR	Coast	V	173
Rhizophoraceae	<i>Rhizophora</i> spp. (8)	T	TR	Coast	V	173
Rosaceae	<i>Eriobotrya japonica</i>	ST	T	Mesic forest	R	28
Rubiaceae	<i>Coffea</i> spp. (2)	ST	TR	Montane	R	28
Rubiaceae	<i>Coprosma robusta</i>	S	ST	Wet forest	V	22
Rubiaceae	<i>Ixora</i> sp.	ST	TR	Wet forest	R	190
Rubiaceae	<i>Ophiorrhiza tomentosa</i>	S	TR	Wet forest	V	167
Rubiaceae	<i>Posoqueria latifolia</i>	ST	TR	Swamp forest	R	86
Rutaceae	<i>Citrus</i> spp. (2)	ST	TR	Agriculture	R	28
Rutaceae	<i>Clausena dentata</i>	ST	TR	Agriculture	R	190
Rutaceae	<i>Fortunella japonica</i>	ST	TR	Agriculture	R	190
Santalaceae	<i>Santalum album</i>	ST	TR	Wet forest	R	2
Sapindaceae	<i>Euphoria longan</i>	ST	TR	Wet forest	R	40
Sapindaceae	<i>Litchi chinensis</i>	ST	TR	Wet forest	R	201
Sapindaceae	<i>Magonia pubescens</i>	ST	TR	Wet forest	R	185
Sapindaceae	<i>Meliococcus bijugatus</i>	ST	TR	Wet forest	R	40
Sapindaceae	<i>Nephelium lappaceum</i>	T	TR	Wet forest	R	28
Sapotaceae	<i>Calocarpum sapota</i>	T	TR	Wet forest	R	28
Sapotaceae	<i>Chrysophyllum cainito</i>	ST	TR	Wet forest	R	28
Sapotaceae	<i>Manilkara zapota</i>	ST	TR	Wet forest	R	28
Sapotaceae	<i>Mimusops</i> sp.	T	TR	Agriculture	R	190
Sapotaceae	<i>Pouteria ramiflora</i>	T	TR	Wet forest	R	185
Sapotaceae	<i>Euphrasia disperma</i>	H	ST	Wet forest	V	28
Scrophulariaceae	<i>Quassia indica</i>	T	TR	Wet forest	R	190
Simaroubaceae	<i>Cola nitida</i>	ST	TR	Mesic forest	R	28
Sterculiaceae	<i>Theobroma cacao</i>	ST	TR	Wet forest	R	28
Surianaceae	<i>Guilfoylia monostylis</i>	T	TR	Wet forest	R	127
Theaceae	<i>Camellia sinensis</i>	ST	TR	Montane	R	28
Verbenaceae	<i>Vitex divaricata</i>	T	TR	Wet forest	R	118
Vochysiaceae	<i>Vochysia honourensis</i>	T	TR	Wet forest	R	185

\*Listed are the taxonomic **family** to which they belong; the **species** (with a number indicating total number of species with trait, if more than one per genus); the **life form** of the adult plant (T, tree taller than 10 m; ST, small tree; S, shrub; V, vine/liana; P, palm; H, herbaceous); the **latitude** or native region of the species (T, temperate; TR, tropical; ST, sub-tropical); the native **habitat** of the species, including agricultural ("ag") if the species is cultivated; **seed status** (R, recalcitrant; V, viviparous; and **source**, the published paper(s) that documents seed status with a germination study).

for germ plasm conservationists, foresters concerned with tropical and temperate forest regeneration, and restoration ecologists. Thus, in devising seed storage schemes, substantial efforts have been devoted to systematically diagnosing types and causes of recalcitrant behaviors (28, 31, 139). Many of the recalcitrant species thus far identified are economically important tropical fruit crops (28) and timber species (184, 201). The degree of recalcitrance exhibited by seeds varies among maternal lines in some species, indicating a genetic component to its control (136).

Until recently, comprehensive accounts of seed dormancy regimes among the angiosperms have been widely scattered throughout the botanical and physiological literature (e.g. 5, 10, 33, 42, 74, 76, 104, 127). However, a few recent compendia provide systematic data on the specific phenomena of vivipary and recalcitrance and on anatomical features, germination characteristics, and habitats shared by predominantly economically important species (28, 42, 190, 191).

Compiling this literature, I enumerate here 78 families, including 195 species in 143 genera, containing members that exhibit some form of vivipary or recalcitrance (Table 1). This feature manifests itself in fully viviparous or cryptoviviparous (e.g. see 173) behavior in 65 species (cf ~50 species noted in 42) and recalcitrance in the remaining 130 species. This list omits the hundreds of species, primarily of tropical wet-forest and riverine habitats, whose seeds germinate within a few days of release but for which their desiccation intolerance has not been established (e.g. 67, 185), as well as taxa for which only one anecdotal account exists.

It is also illuminating to compare these types with other species that sprout viviparously under certain circumstances. Some of these species are recalcitrant, while others are normally dormant. For example, seeds of many crop plants, including wheat, rice, maize, sorghum, and barley, that are subjected to unusually high humidity or to flooding will exhibit precocious, preharvest sprouting (5, 145, 176). The external cue for such behavior in these species is an abundance of water, often enhanced by warm temperatures. Although the propensity to sprout prematurely is dependent on environmental stimuli, susceptibility to these cues varies heritably among cultivars and thus is genetically based (192). In addition, a small set of mutant genotypes also produce seeds that germinate prematurely on the parent plant. Mutants of tomato, wheat, corn, and *Arabidopsis* exhibit viviparous phenotypes that reflect altered production of phytohormones, reduced sensitivity to dormancy-inducing phytohormones, and modified embryonic and adult water relations (36, 69, 80, 98, 109, 119, 149, 183). Studies of both precocious sprouters and mutants suggest that these nondormant phenotypes may result from alterations in hormonal biosynthetic or signal transduction pathways. Many precocious sprouters and viviparous mutants exhibit nondormant behavior that is anomalous with respect to the normal seed behavior of the species. However, I make reference to them from time to time in this review because the biological phenomena behind these unusual phenotypes may, in some cases, be similar to those operating in viviparous and recalcitrant taxa.

## EMBRYO DRYING DISTINGUISHES DORMANT SEEDS FROM VIVIPAROUS AND RECALCITRANT SEEDS

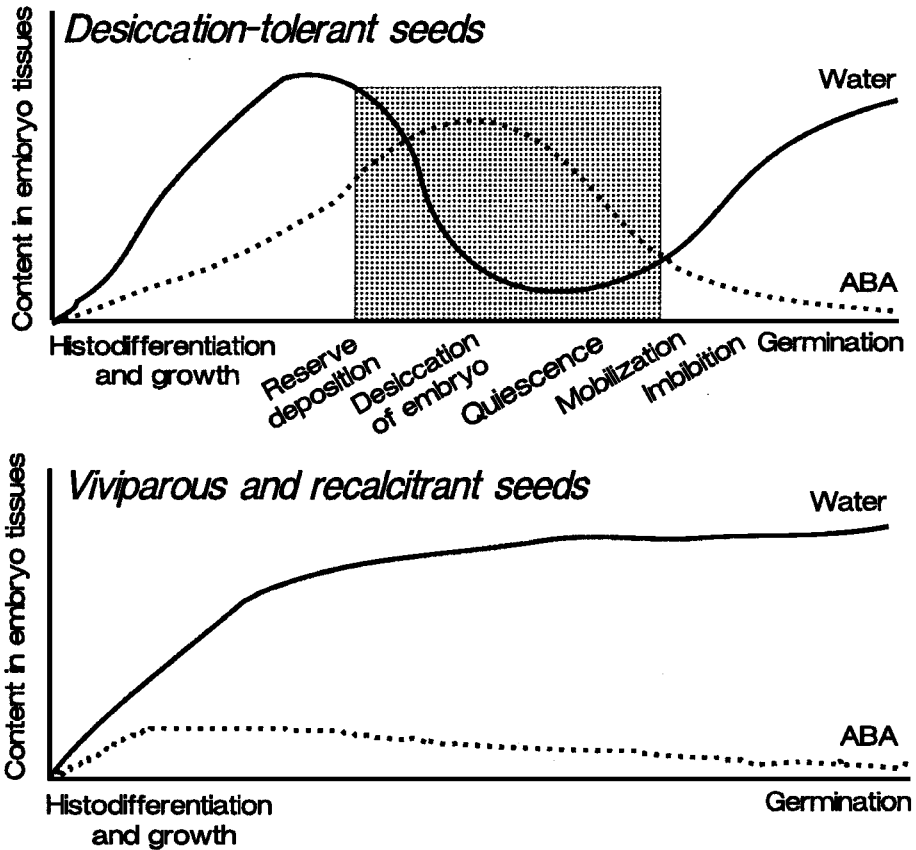
Viviparous and recalcitrant seeds differ in fundamental ways from seeds that undergo dormancy. Dormant seeds exhibit the following generalized chronology of development: (a) embryo growth and tissue differentiation; (b) seed expansion, reserve deposition, and vacuole filling; (c) internal desiccation, organellar de-differentiation, and membrane stabilization; (d) metabolic quiescence; (e) imbibition, reserve mobilization, and resumption of metabolism in response to environmental signals; and (f) germination, commonly by root protrusion through the seed coat (Figure 1). Germination commences when intensive metabolic activity is regained following dormancy. In contrast to dormant species, viviparous and recalcitrant taxa lack the third step of maturation drying and consequent metabolic quiescence and proceed directly to the germination phase.

Viviparous and recalcitrant embryos maintain high tissue moisture contents throughout ontogeny (146; Figure 1). Water is critical to embryo metabolism and development; indeed, its uncontrolled loss exerts deleterious impacts on cell structure, mitotic growth, and biochemistry in all plant tissues. Seed germination, growth, DNA integrity, protein synthesis, membrane structure, organellar formation, and normal embryo development are disrupted when internal hydration levels drop below critical thresholds, which themselves vary among species (3, 95, 113, 131). Loss of metabolic water during prolonged drying is accompanied frequently by fusion of vacuoles, vesiculation of the endoplasmic reticulum, and free-radical peroxidation of lipid and protein components of cell membranes, leading to eventual cellular collapse (77, 129, 132, 156). Much of this damage is manifested during rehydration. Both the rate of dehydration and the absolute percentage of water lost determine the extent of tissue damage sustained by desiccating embryos (40, 50, 51). All seeds are intolerant to premature drying early in their development, but dormant seeds acquire tolerance to slow desiccation within days after fertilization and increasing tolerance to rapid drying as the embryo ages, whereas recalcitrant seeds never do (Figure 1). Mechanisms conferring desiccation tolerance on the maturing seed have been inferred from numerous studies that use hormonal mutants, endogenous manipulation of water levels and hormone activities, and exogenous applications of hormones to excised embryos (97). The acquisition of desiccation tolerance during mid- to late embryogenesis has been correlated with increases in three substances with related activities: abscisic acid (ABA), dehydrin proteins, and oligosaccharides (Figure 2). Considerably less is known about the status of these substances in naturally desiccation-intolerant species.

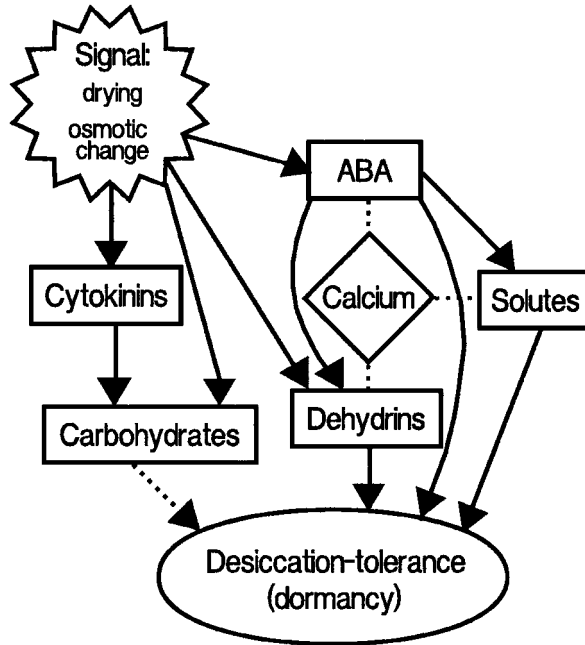
## ROLES OF PHYTOHORMONES IN EMBRYO DRYING

### Abscisic Acid

The phytohormone ABA appears to play a central role in preparing embryos for maturation drying before dormancy. In many desiccation-tolerant seeds, levels of



**Figure 1** A graphical comparison of the dynamics of water and abscisic acid (ABA) in recalcitrant and viviparous (desiccation-intolerant) and dormant (desiccation-tolerant) seeds. Recalcitrant and viviparous embryos cannot dry, and they do not enter a dormant phase. Desiccation-tolerant embryos, by contrast, are capable of drying. While not all inherently desiccation-tolerant embryos enter dormancy in nature, embryos of all naturally dormant plant species show some form of desiccation tolerance. In dormant seeds (*upper diagram*, after 13), water content increases to a peak at the onset of reserve deposition, drops during maturation drying, remains low throughout dormancy, then rises again during imbibition. ABA content increases as the seed dries, but does not necessarily remain high during dormancy. *Lower diagram* (after data from 51, 95) shows the hypothesized accumulation of high levels of water during histodifferentiation in desiccation-intolerant seeds, levels that remain high throughout development. Metabolic quiescence does not occur. ABA levels may peak early during histodifferentiation, but generally remain low throughout maturation.



**Figure 2** Linkages among multiple pathways for regulating desiccation tolerance in plant tissues, including seeds. An environmental signal that induces a change in osmotic status triggers production of the phytohormone abscisic acid (ABA) and its cofactor, calcium, which in turn transduces signals for the release of compatible solutes and transcription of dehydrin class proteins that protect membranes during desiccation stress. Independent pathways may lead to increased cytokinin production and creation of carbohydrate sinks within dehydrating tissues. Together, these linked mechanisms confer desiccation-tolerance on tissues, a prerequisite for dormancy in embryos.

ABA peak either once or twice during mid-embryogenesis (Figure 1). These peaks in ABA levels coincide with the onset of the maturation drying that is prerequisite to dormancy and subsequent germination. ABA may be supplied maternally at first, but later is produced endogenously in the embryo (81).

Several lines of evidence suggest that ABA is necessary (but not sufficient, in some cases) for the acquisition of desiccation tolerance and entry into dormancy. Seeds of ABA-deficient mutants of corn (*vp*), *Arabidopsis* (*abi*), *Nicotiana plumbaginifolia* (*iba*), wheat (*EH-47*), and tomato (*sitiens*) exhibit reduced protein accumulation and lack of dormancy frequently leading to viviparous germination (13, 60, 93, 98, 101, 107). Preharvest sprouting varieties of sorghum also exhibit abnormally low levels of endogenous ABA relative to sprouting-resistant cultivars (161). Embryos of naturally occurring recalcitrant species, including *Theobroma cacao* (135), *Quercus robur* (57), *Hopea odorata* (64), and *Machilus thunbergii* (112), as well as several species of mangroves (halophytic tropical trees) that

are viviparous, exhibit low quantities of ABA throughout embryo development (49, 52, 53).

Artificial manipulation of ABA levels also modifies desiccation tolerance and consequent dormancy in seeds. For example, exogenous addition of ABA induces and prolongs desiccation tolerance in cultured embryos, ABA-deficient mutants (121), and recalcitrant species (58) and also inhibits germination (148, 200). Likewise, application of ABA-inhibitors at early stages of embryo maturation induces precocious germination in seeds (200).

Desiccation intolerance also may, in certain cases, be associated with a lack of sensitivity to ABA. Embryos of some recalcitrant species (65), preharvest sprouters (161), and one naturally viviparous species (163) exhibit reduced sensitivity to the normally inhibitory effects of ABA on metabolic activity and germination. Likewise, ABA-insensitive mutants are desiccation intolerant and germinate viviparously (36, 119, 183). More information on hormonal sensitivity is needed for a wider range of species (177). Together, these findings suggest the hypothesis that ABA is integrally involved in preparing the mature embryo for desiccation in anticipation of seed dormancy and, conversely, that ABA levels or sensitivity may be lacking in recalcitrant or viviparous species.

Both ABA concentrations (Figure 1) and embryo tissue sensitivity to ABA first peak and then diminish quickly following drying, however, indicating that ABA initiates, but does not necessarily enforce, long-term dormancy (95). Both ABA and external osmotic potentials may constitute analogous and complementary, but separate, signals to the embryo (95). Precise mechanisms by which ABA controls osmotic balance in embryo cells are largely unknown, as cellular ABA receptors have proven elusive (109, 194). ABA may regulate osmoticum in the seed directly (63). Alternatively, ABA may function primarily indirectly as a signaling molecule that binds to a membrane-bound ABA-response element (e.g. see 8), initiating a phosphorylation cascade that up-regulates gene expression for a constellation of stress-related proteins (19). Both free and membrane-bound calcium ions ( $\text{Ca}^{2+}$ ), ubiquitous in plant cells, may help transduce ABA signals (155), a point to which I will return later in this review. ABA has been detected in all seed components, and its regulatory action in seed dormancy may not be restricted to embryonic tissues alone. Communication of ABA among endosperm and embryo to coordinate tissue dehydration, for example, may occur (78).

The pleiotropic (e.g. see 56) nature of ABA action in different plant compartments must be taken into account when studying changes in its production in isolated plant tissues. ABA, like other phytohormones, regulates suites of phenotypic traits in plants and coordinates integrated responses of plants to multiple, interacting environmental stresses (25; Table 2). In addition to its activities in seeds, abscisic acid regulates desiccation tolerance in vegetative tissues of mature plants (19, 129). Evidence for this role comes from studies of mature ABA-deficient mutants, which are prone to wilting, drought rhizogenesis, and other manifestations of impaired water balance. ABA levels transiently increase in roots of plants subjected to flooding, salt stress, and drought, and ABA may be transported to leaves as a signal to induce stomatal closure (36, 202) and to shoots to promote

**TABLE 2** A summary of basic hormone actions in plants

<b>Structure</b>	<b>Cytokinins</b>	<b>Auxin</b>	<b>Gibberellins</b>	<b>Abscisic acid</b>	<b>Ethylene</b>
Organelle/ wall	Tonoplast integrity; chloroplast maturation; increases wall plasticity	Wall loosening through proton release	Increases cell wall elasticity	Regulates ion permeability of cell/tonoplast membranes	Increases tonoplast permeability; degrades cell walls
Whole cell	Reduces free radical production; promotes release of cellulases; promotes mitosis; increases turgor	Up-regulates proton pump; induces release of cellulases	Up-regulates sugar-digesting enzymes; Increases osmotic potential; promotes mitosis; promotes cell elongation	Down-regulates proton pump; promotes dehydrin protein production; promotes calcium import	Inhibits chlorophyll binding; up-regulates cellulase; promotes radial expansion; hastens cell senescence
Shoot meristem	Promotes lateral bud formation	Confers apical dominance; promotes epidermal growth	Releases bud dormancy; floral induction	Enforces bud dormancy	Promotes epinasty; slows stem growth; slows hook opening
Stem	May promote elongation	Promotes phototropic and geotropic bending	Promotes bolting and elongation	Unknown	Increases thickening; production of air spaces
Leaves	Delays senescence	Unknown	Hastens maturation; promotes growth	Wilting; stomatal closure; abscission	Promotes curling; hastens senescence
Flowers	Unknown	May inhibit flowering	Induces flowering; day-length response; vernalization; sex expression	Unknown	Flower curling; promotes female sex expression; may influence timing of flowers
Fruits/seeds	Hastens cory/ledon maturation	Unknown	Promotes parthenocarpic fruit production; promotes seed germination	Enforces seed dormancy	Hastens fruit ripening
Roots	May promote meristem growth and root production	May promote meristem growth; promotes adventitious root production; regulates geotropism; up-regulates ethylene	Inhibits adventitious root production	Inhibits root growth; regulates membrane permeability to ions	Inhibits elongation; increases adventitious root number; aerates roots through production of aerenchyma

elongation during submergence (16). In roots and stomata, as in seeds, ABA alters cellular permeability to water and up-regulates production of versatile stress proteins (84). Together, ABA and osmotic stimuli can induce expression of salt-responsive genes (64).

Major evolutionary modifications in ABA levels and action in certain plant tissues may be necessitated by selection pressures experienced by plants as they colonize novel habitats via population differentiation and speciation (189). For example, high ABA concentrations in roots or leaves may be required to maintain whole-organism water balance under conditions of water stress or salinity. Because the plant is an integrated unit, however, high ABA levels in vegetative compartments could potentially inhibit or hinder metabolic processes in reproductive tissues. Plant species subjected to chronic stress may compartmentalize ABA production, activities, and tissue sensitivities, such that up-regulation of ABA in one sector does not impact another sector and cause a cascade of linked responses to ensue (24, 25). Evidence supporting this hypothesis comes from a study of four unrelated families of mangroves (49). These mangroves exhibit moderate to high levels of ABA in vegetative compartments and maternal tissues of the fruit, but very low ambient levels of ABA in the embryo throughout development (relative to nonviviparous related species). Vivipary and reductions in ABA have both arisen in mangrove lineages coincident with acquisition of the halophytic habit (92, 152, 173). A loss of desiccation tolerance and consequent seed dormancy in naturally occurring wetland or semi-aquatic species, precipitated by a significant reduction of ABA in the seed relative to that present in vegetative tissues, may be one notable consequence of evolutionary changes in ABA physiology that enable certain species to persist under conditions of osmotic stress (49, 52).

## Other Phytohormones

ABA is one of five recognized phytohormones critical to plant growth and development (Table 2). Evidence for a role of other phytohormones in controlling desiccation tolerance or dormancy is scanty and somewhat inconsistent, however. For example, active gibberellic acids (GAs) are known to promote embryo germination and antagonize ABA activity (83, 165). Likewise, increased sensitivity to GAs may accompany or precede germination (106), and application of GA inhibitors can induce dormancy in formerly nondormant seeds (96). One might hypothesize that precociously germinating species of all types discussed here would show elevated levels or differing forms of gibberellins throughout embryogeny. Dormant and nondormant varieties of beech, for example, appear to possess different suites of GAs synthesized from divergent biochemical pathways (55). However, although active GAs have been detected in young embryonic axes of a viviparous mangrove species, *Rhizophora mangle* (133), they were not unusually high relative to nonviviparous species, nor is there consistent evidence that gibberellins are significantly elevated in recalcitrant seeds or perform functions different from those observed in dormant seed types (53, 125). Vivipary has not

been reported among constitutive GA mutants (83, 98). Furthermore, GAs often cannot induce germination in embryos of some desiccation-tolerant species unless maturation drying, accompanied by peaks in ABA production, has first occurred (54, 95). Many facets of GA signal transduction and its role in seed physiology remain to be clarified (172).

Auxins, specifically indoleacetic acid, are found in all seed tissues, most abundantly in the cotyledons and the pericarp, which are both reserve-accumulating tissues. However, auxin concentrations in tissues generally decline as the embryo matures, and auxin does not appear to play a major role in either dormancy or germination. Its concentrations in recalcitrant seeds do not consistently differ from those of desiccation-tolerant seeds (53, 125).

Cytokinins are implicated both in the reserve accumulation phase of embryo development and in maintaining cell growth and division throughout embryogeny. Cytokinins promote cell division by accelerating rates of protein synthesis and decreasing the duration of cellular interphase (36). In seeds that undergo dormancy, cytokinins are most abundant during early histodifferentiation of the embryo—a period of rapid cell division and growth—and later in embryogeny, when they may influence seed germination through complementary signal transduction pathways sensitive to light (169). Cytokinins are present in relatively high concentrations in the recalcitrant seeds of *Citrus* spp. (43), *Avicennia marina* (53), and several other viviparous species of mangroves (46), indicating that they may be involved in maintaining continual cellular activity. Cytokinins may also help halophytes to overcome salt-induced inhibition of germination (70). Their role in seed metabolism and precocious germination deserves further study.

Ethylene exerts limited effects on embryo metabolism, and mechanisms of its action are largely unknown (94). When it attains high concentrations inside the testa, ethylene sometimes is credited with breaking dormancy (103). Ethylene production accelerates as fruits ripen, but this increase appears to be decoupled from the maturation of the embryo itself. Although ethylene production apparently rises during maturation drying of certain seeds, its dynamics vary between congeneric species, and its role in desiccation tolerance is uncertain (88). In fact, ethylene impedes germination of the recalcitrant seeds of *Quercus robur* (58). In flooded or aquatic habitats, ethylene concentrations in submerged organs (especially roots) can attain high levels due to its slowed diffusion from waterlogged tissues. Because recalcitrant and viviparous wetland taxa often inhabit seasonally or chronically flooded environments (Table 1), a possible role for ethylene in altered seed physiology warrants more investigation.

In determining the roles hormones play in the regulation and evolution of a complex life history trait such as seed dormancy, it is imperative to quantify the following: (a) hormone concentrations at the site of action, (b) sensitivity of the tissues involved in complex responses, and (c) relative significance of hormonal control assessed against a background of other controlling influences (177, 197). Manipulative tests of hormone action must be coupled with genetic analysis of loci involved in producing hormones and transducing their signals and performed in a broad array of desiccation-intolerant species.

## ROLES OF PROTEINS IN EMBRYO DRYING

Several common proteins are implicated in the acquisition of desiccation tolerance (84). Many of these proteins are produced in a variety of vegetative and seed tissues during periods of drought stress, although similar responses occur during exposure to other stresses including salinization, heat-shock, and chilling. It is of interest that many of the recalcitrant and viviparous seeds that lack these proteins are also quite sensitive to chilling, suggesting that these proteins have multiple protective functions.

A specific class of dehydration proteins becomes prevalent in desiccation-tolerant seeds as maturation drying commences, ABA levels increase, and water content declines. These proteins [Em proteins (117), late-embryogenesis-abundant (LEA) proteins (39), and ABA-responsive (Rab) proteins (155)] are referred to as “dehydrins” throughout the literature (30). They have been identified in diverse species including cotton, several cereals, legumes, tomato, pine, *Arabidopsis*, “resurrection” plants in several families, and mosses (84, 95, 100). Their expression chronology, sequence motifs, biochemical characteristics, and hydrophilic nature are highly conserved within and among diverse taxa (30). Dehydrins bind water, sequester ions amassed during desiccation, and coat membrane components to preserve a stable configuration during water loss (30, 39). They also function as ABA-responsive promoters of gene expression (109, 117). ABA-deficient viviparous mutants show reduced levels of these proteins throughout embryogeny (116), indicating that ABA signaling may be prerequisite to the production of dehydrins. Dehydrins are absent from several recalcitrant and viviparous species (52, 53). However, their presence in some recalcitrant species, including *Quercus* species and wild rice, suggests that dehydrins are necessary, but not sufficient, to achieve desiccation tolerance in seeds (18, 59). Likewise, some ABA-insensitive mutants of *Arabidopsis* show little apparent reduction in dehydrins (60). Thus, ABA may not constitute the sole signal for dehydrin up-regulation in this complex pathway (44).

## ROLES OF CARBOHYDRATES AND COMPATIBLE SOLUTES IN EMBRYO DRYING

### Carbohydrates

Carbohydrates are a dominant component of all plant cells, providing the foundations of cellular structures, the fuel for cellular activities, and the solutes for maintaining osmotic equilibrium in the cytosol. The importance of various carbohydrates to the acquisition of desiccation tolerance by plant tissues, especially seeds, is continually debated, principally because the precise mechanisms by which sugars confer desiccation tolerance are still largely unknown. Certain soluble sugars increase in concentration within embryos of some species as dehydration commences (15, 108) and decrease in other species as desiccation tolerance is lost

(102). However, this phenomenon appears to be both species-specific and dependent upon the rate of drying applied to the seed (168). Sugars such as sucrose can promote desiccation tolerance by stabilizing cell membranes, either by replacing water with hydroxyl groups (35, 79, 95) or by vitrifying—forming highly viscous, aqueous glass (187). Seeds of desiccation-intolerant species, therefore, may be deficient in these sugars throughout development (46). However, evidence of water replacement and vitrification has been detected in seeds of recalcitrant species (187). Some recalcitrant seeds exceed desiccation-tolerant seeds in their oligosaccharide content (12, 51), for example, and consistent differences in sugar content between viviparous and nonviviparous mangroves have not been found (193). Farrant et al (51) proposed a link between high levels of cytokinins in the embryo and an accelerated rate of sugar import, as cytokinins are implicated in metabolic sink formation. Cells that are actively respiring, growing, and dividing also become sinks for carbohydrates, especially sucrose (which functions doubly to fuel metabolic activities of cells and, as a compatible osmolyte, to maintain turgor). Likewise, modifications in ABA production or action in viviparous, recalcitrant, early sprouting or mutant seeds may also affect sugar metabolism. For example, ABA inhibits acid invertase, sucrose synthase, and sucrose phosphate synthase activities in certain cells (29), acting antagonistically to cytokinins. Thus, a reduction in ABA, coupled with an increase in cytokinins in these embryos, may be associated with changes in rates of phloem unloading and sucrose processing. Mutants exhibiting altered carbohydrate biosynthetic pathways would be particularly useful study subjects in this regard, but their seeds have not yet been examined explicitly for desiccation intolerance (196). Because levels and types of sugars cannot be linked consistently with desiccation tolerance, it is unlikely that differences in oligosaccharide concentrations alone can distinguish recalcitrant and viviparous seeds from other types (129).

## Solutes

Since viviparous and recalcitrant embryos do not normally develop tolerance to osmotic stress associated with maturation drying, it is logical to ask whether ion concentrations are consistently different in cells of these embryos and whether these differences contribute to the inability of these embryos to withstand drying. Simple inorganic ions, such as sodium, potassium, and calcium, can accumulate at various levels in drying cells as a function of water loss. They may be selectively released from vacuoles or selectively concentrated through preferential uptake by ion-specific membrane transporters (150). Nondormant barley varieties, for example, show higher cellular conductivity to potassium than dormant types (182). The preferential accumulation of potassium vs sodium in vegetative tissues has been well documented in salt- and drought-tolerant halophytes, including mangroves (6), in which active transport of potassium ameliorates the potential deleterious effects of sodium on photosynthetic processes. Joshi et al (90) observed that sodium:potassium ratios are lower in viviparous embryos than in

nonviviparous mangrove embryos and proposed that this preferential uptake of potassium in competition with sodium reflects precocious development of salt tolerance. In contrast, observations that solutes decrease over time in viviparous embryos have led to the suggestion that viviparous reproduction is a desalinating process (203).

In addition to their ionic function in regulating osmotic potential, calcium ions are ubiquitous intracellular second messengers in plants, and they help to transduce ABA signals into stimuli for gene up-regulation (109, 195). Calcium inhibitors, as well as reductions in cytoplasmic calcium contents, inhibit production of ABA-responsive stress messenger RNAs (153). It is of interest, therefore, that calcium appears to occur at lower concentrations in the embryos of viviparous mangroves than those of nonviviparous nonmangroves (46). However, Joshi et al (90) found little difference in calcium levels in embryos of viviparous vs nonviviparous mangroves, indicating that reduced intracellular calcium may be more a characteristic of mangroves in general than a correlate of the viviparous habit. Likewise, abscisic acid-deficient mutants of *Arabidopsis* show similar responsiveness (compared with wild types) of internal calcium levels to applied salt stress, indicating that calcium responds to osmotic and ABA signals independently (34).

A small spectrum of compatible solutes (soluble compounds of low charge that do not harm cellular metabolism even at high concentrations) is produced in response to several stressors, including desiccation, salinity, and cold. In their evolutionary conservatism, they are reminiscent of the broad-response stress proteins that serve both as osmoregulatory solutes and as structural osmoprotectants (17, 84). Although compatible solutes are known to contribute to the development of desiccation tolerance in vegetative tissues, their roles during maturation drying in seeds only rarely have been investigated. Because proline can constitute a quarter or more of the amino acid profile of reproductive tissues, it has received the most attention. In desiccation-tolerant varieties of *Arabidopsis thaliana*, proline is found most abundantly in seed tissues with relatively low water content, and it is up-regulated in embryonic tissues subjected to artificial water stress or applications of exogenous ABA (27). Specifically focusing on recalcitrant seeds, Lin & Chen (112) found that low levels of proline characterized the desiccation-intolerant embryos of *Machilus thunbergii*. Viviparous mangroves do not appear to be impaired in their production of compatible solutes in vegetative tissues, but levels in embryonic tissues are unknown (138).

In summary, while considering physiological correlates with embryo drying in plant lineages, I have discussed certain regulators that are likely to be shared by several plant types that are intolerant to maturation drying. First and perhaps foremost, the recalcitrant and viviparous seeds studied to date most consistently exhibit either reduced levels of, or sensitivity to ABA, or both. Studies of the acquisition of desiccation tolerance in vegetative tissues and seeds suggest that changes in the production of stress proteins (particularly the late-embryogenesis-abundant dehydrins), cytokinins, sucrose, ions, and compatible solutes may coincide with either imposed water stress or ordinary maturation-related drying. A reasonable

hypothesis, therefore, is that the loss of desiccation tolerance in recalcitrant and viviparous phenotypes is attributable to alterations in the regulation of one or many of these (physiologically linked) characters. Figure 2 illustrates how principal phytohormones, proteins, and solutes may interact during acquisition of desiccation tolerance and how reductions in their production can result in desiccation intolerance.

## ECOLOGICAL AND STRUCTURAL COMMONALITIES AMONG RECALCITRANT AND VIVIPAROUS SPECIES

In addition to shared physiological characteristics, several broad ecological commonalities emerge from qualitative surveys of desiccation-intolerant taxa (Table 1). The taxa identified span a broad range of plant life forms including shrubs (12%), palms (5%), lianas/vines (2%), herbs (9%), and epiphytes (1%), with canopy trees (45%) and small understory trees (26%) constituting the majority. In terms of habitat, most recalcitrant and viviparous species (89%) occupy wet-forest, riverine, flooded, or coastal environments. Most species (79%) are native to the tropics [a recent review (10) posits that, in general, more than 60% of species of wet tropical zones possess minimal dormancy, but less is known specifically about their desiccation intolerance]. Few of the desiccation-intolerant taxa identified here occur in seasonally cold climates (15% of total), and most of these temperate-zone species inhabit riverine or swamp habitats (e.g. *Potamogeton*, *Caltha*, and *Sagittaria* species (10)). A majority of the viviparous species occupy coastal tropical zones, especially mangrove forests, that are inundated daily or seasonally by tides. Many of the desiccation-intolerant taxa produce seeds that mature during tropical monsoons and rainy seasons and are unlikely to experience dry conditions.

These disparate species also share several fruit and seed characteristics, which contrast with seed traits of closely related dormant taxa. Over 70% of viviparous and recalcitrant species produce seeds that occur singly within the fruit. Their seeds are typically large (exceeding 4 cm in length). While the typically fleshy tissues surrounding the seed are sometimes soft, permeable to water, and high in moisture content, hard testae or exocarps occur among more than 40% of these species. Many (74%) of these species possess large embryos that occupy more than half the volume of the seed. Endosperm volume is correspondingly small or nonexistent in the majority of these species, and exalbuminous embryos that are independent of the endosperm are common. However, several viviparous mangroves possess a well-developed endosperm (32, 99), which in members of the Rhizophoraceae may even physically displace the embryo and hasten its bursting from the fruit (91). Copious cotyledonary starch reserves have also been noted among the recalcitrant taxa surveyed by von Teichman & van Wyk (191). Of interest is whether cotyledonary tissues function as storage tissue for the

embryo and/or whether they provide nutrients to fuel continual metabolic activity (53).

We might expect large (especially viviparous) embryos to be supplied initially by maternal resources, but specific mechanisms of maternal transfer have not been studied. Certain viviparous species of mangroves appear to show discrete haustorial transfer tissues that do not occur in putatively ancestral, upland relatives (72, 164, 178, 199). Elaboration of maternal communication to the embryo may have proceeded during evolution once vivipary evolved in these lineages, as has been demonstrated in the Rhizophoraceae (92, 199). Alternatively, intensive maternal provisioning may preclude dormancy because water and nutrients are continually supplied to a metabolically active embryo. Is altered ABA production a consequence of modified modes of communication and water relations between the maternal plant and embryo among certain species of flooded or saline environments? Mature plants of these recalcitrant and viviparous species produce ABA in vegetative tissues, a likely mechanism for promoting tolerance to osmotic stress (16, 49), yet young embryos appear to postpone ABA up-regulation until after dispersal or establishment has occurred. As proposed earlier, physiological traits in the developing seed may evolve as a consequence or by-product of maternal adjustments to a range of external stimuli and selection pressures, including mechanisms of compartmentalizing hormonal production and function. However, mature plants and seeds of a wider range of recalcitrant and viviparous species must be studied to establish the generality of this hypothesis.

## THE EVOLUTIONARY STATUS OF VIVIPARY AND RECALCITRANCE

To assess the evolutionary significance of correlations among desiccation intolerance, other seed characteristics, and habitat, it is necessary to establish whether these characteristics are ancient or recent evolutionary developments and whether they consistently appear simultaneously during evolution. Recalcitrance *sensu lato* has been viewed as pleisiomorphic based on its putative correlation with other primitive (e.g. see 190, 191) characteristics such as woodiness and a tropical habitat. It is difficult to assess the precise concordance of these characteristics in relation to desiccation intolerance at the species level, however, as previous authors have compiled their surveys at the level of families, providing only very coarse resolution (190, 191). Takhtajan (166) postulated trends in endosperm evolution, seed coat simplification, and dispersal modes that can indicate the evolutionary age of taxa and the relative status of seed traits, but simultaneously notes the occurrence of parallel character states in lineages of both ancient and recent origin. The seeds surveyed in the present review exhibit a variety of ancestral and derived traits according to Takhtajan's criteria. Phylogenetic evidence suggests that vivipary and recalcitrance are not always relict characteristics of ancient taxa;

rather, these traits have evolved repeatedly in descendants of desiccation-tolerant taxa. Recent phylogenies for the Araceae (62), Aceraceae (1), Araliaceae (130), and Rhizophoraceae (152), for example, place the recalcitrant or viviparous taxa in recent or terminal clades, while others addressing the Arecaceae conflict on the precise placement of the viviparous, monotypic genus *Nypa* (26, 179). Recalcitrance or vivipary occurs only in a single known species in each of 37 (47%) of the families, and 122 (85%) of the genera are monotypic for this trait. Thus, this characteristic has not proliferated among congeneric taxa within families, except among the mangrove members of the Rhizophoraceae, Avicenniaceae, Myrsinaceae, and Plumbaginaceae, as well as members of the species-rich Dipterocarpaceae native to tropical wet-forest habitats. Considering the fact that recalcitrance or vivipary occurs primarily in single taxa or genera within families, the most parsimonious explanation for their presence points to a few convergent losses of desiccation tolerance. A broader, quantitative examination of the evolutionary status and linkages among vivipary and recalcitrance awaits both the development of high-resolution phylogenies for more of the plant families listed in Table 1 and the systematic characterization of desiccation tolerance in their sister taxa.

## EVALUATING COSTS AND BENEFITS OF VIVIPARY AND RECALCITRANCE

The benefits of seed dormancy as a means of maximizing seed output and optimizing dispersal distance and time have received most attention in the ecological and evolutionary literature (45, 75, 86, 144, 186, 188, 198). Similar models have been applied to animals, such as sponges and copepods, whose gemmules and eggs, respectively, exhibit long-term dormancy (73, 141). In contrast, the lack of dormancy has received comparatively little theoretical attention (42, 67, 85, 185).

When considering the putative advantages and disadvantages of particular modes of reproduction to explain their adaptive value, evolutionary biologists have emphasized three seed features as critically important to subsequent plant fitness: (a) maternal carbon costs of reproduction balanced against the early carbon needs of the offspring, (b) seed quantity (maternal fecundity) vs seed quality (namely, seed size and nutrient content), and (c) the value of dormancy or dispersal for ensuring establishment in spatially and temporally heterogeneous environments. In investigating recalcitrance and vivipary—the lack of dormancy—with reference to these features, authors have postulated that early germination proffers adaptive benefits and should also be associated with larger seed size, directed dispersal, long adult life spans, and less specialization to microhabitats (61, 144, 154, 162, 196, 188, 190). Several authors have postulated that dormancy and concomitant dispersal in time and space offer no selective advantage to seeds released into spatially or temporally homogeneous habitats or into coarsely mosaic environments where compatible patches are separated widely in space

(42, 110, 137, 171, 181). The seed phase can be short-lived, and selection pressures to promote the evolution of dormancy do not exist in these environments.

When one looks critically at the hypothetical benefits of vivipary and recalcitrance, particularly in the context of the ecology of specific species, one also notes the considerable costs of these modes. For example, large, viviparous seedlings of species such as mangroves may enjoy a considerable head start due to their early germination, assimilation of carbon from both maternal and (possibly) atmospheric sources (91), and prodigious growth before dispersal. Early germination is thought to expedite rapid rooting of mangroves following propagule release (114), for example, or to promote the salt tolerance of seedlings (89, 157). However, neither propagule size nor levels of nitrogen provisioning of viviparous mangrove propagules is correlated with subsequent establishment success or rates of growth (46, 111), and seedlings produced in a hypersaline maternal environment do not fare better in high-salinity growing conditions than do seedlings growing on trees of less saline areas (157). Other hypotheses suggest that, in nondormant species, establishment immediately follows reproduction, which itself is cued to environmental conditions that will optimally foster seedling growth (4, 159). However, this does not hold true consistently; some viviparous mangrove species reproduce copiously during certain seasons but undergo massive seedling mortality in most years (41, 47). Alternatively, others have proposed that large, nondormant seeds of tropical trees may be less inhibited by a lack of light (both a phytochrome germination signal and a critical resource for growth) in deep forest understories (185). However, studies of viviparous mangrove species show that early photosynthesis, growth, and survivorship are quite sensitive to light availability (41, 47). Another theory postulates that dormant seeds lingering in soil banks are quickly eaten or parasitized and that rapid germination enables accelerated establishment and escape from seed predators (126, 170). However, both predispersal and postdispersal predation of viviparous mangrove embryos, for example, can significantly reduce reproductive success (48, 147). Likewise, early emergence time is not strongly associated with resistance to herbivory in tropical rain forests (134).

Studies focusing on the adaptive value of these reproductive strategies yield evidence that precocious germination can also exact costs by entailing substantial maternal investment of carbon and nutrients in supplying a metabolically active embryo, reducing the quantity of seeds produced relative to the cost of provisioning each seed, and limiting dispersal latitude while hastening establishment of the vulnerable, metabolically demanding embryo. Comparative studies need to address mechanisms by which vivipary and recalcitrance have arisen convergently in so many unrelated taxa and, conversely, why such a seemingly advantageous strategy has not proliferated among temperate-zone halophytes and other angiosperms. Indeed, many (especially temperate) halophytes and freshwater wetland plant species exhibit desiccation tolerance and dormancy (180). A fruitful line of research would focus on specifically comparing the physiology and relative fitness of desiccation-tolerant and desiccation-intolerant taxa within these environments (82, 174).

## INTEGRATING PHYSIOLOGY, ECOLOGY, AND EVOLUTION IN UNDERSTANDING SEEDS

To refine hypotheses about costs and benefits of recalcitrance and vivipary, we must critically examine whether desiccation tolerance actually confers higher survivorship, establishment success, or fitness across a range of species within particular habitat types and across the lifetimes of plants. To address the evolution of complex traits generally, we must (*a*) understand physiological pathways that control single traits and the linkages among them, (*b*) identify other traits with which the character in question is consistently associated across lineages, (*c*) determine that it has arisen independently in multiple lineages (and is not a by-product of phylogenetic relatedness), (*d*) investigate whether the evolutionary appearance of the trait within lineages consistently coincides with the evolutionary colonization of the habitat in question, and (*e*) compare the fitness of species sharing the same selective pressures that exhibit and do not exhibit the trait.

To develop coherent and credible optimality theories addressing the evolution of seed traits, we need to clarify genetic, physiological, and ecological similarities among species and learn from their differences (160). Recent promising comparative studies have begun to explore the physiological bases for convergent traits appearing in diverse lineages (46, 49, 52), identify genuine suites of correlated seed traits occurring within lineages (45, 134, 158), and investigate the transgenerational adaptive significance of seed traits and maternal effects (123, 162).

As Voesenek & Blom (189) and Blom (16) recently observed, a closer look at the status and evolution of plant hormones may help us to predict the appearance of traits under certain environmental conditions, to understand linkages among traits, and to manipulate traits to promote fitness. Within the seed, phytohormones figure importantly in controlling embryogenesis, dormancy, and germination. Hormonal pathways and sensitivities are pleiotropic and heritable, and hence they are subject to selection (109, 136). Little is as yet known, however, about how hormonal regulation of seed and whole-plant ecophysiology has evolved in angiosperms or has contributed to trends in dormancy regimes or contrasting seed bank dynamics in different environments (24, 25, 189). Insofar as hormones modulate source-sink relationships between the seed and parent plant, they may shape the evolution of life history tradeoffs in maternal investment during seed maturation (20, 143, 151). Indeed, the study of evolutionary physiology in general has lagged behind that of morphological evolution because (*a*) the precise nature of homology in physiological and biochemical traits is challenging to identify, (*b*) linkages between morphological homologies and their physiological correlates are difficult to delineate, (*c*) the plasticity and transience of physiological states demand that traits be characterized for a full range of conditions when comparing among taxa, and (*d*) physiological states generally do not leave a fossil record (21). Nevertheless, the comparative study of hormonal physiology in plant lineages is made possible by advances in phylogenetic methodology and by an exponentially

increasing knowledge of hormonal mechanisms at both molecular and whole-organism levels.

## ACKNOWLEDGMENTS

I thank E. A. Kellogg, N. M. Holbrook, F. A. Bazzaz, A. M. Ellison, D. G. Fautin, L. A. Meyerson, and D. Stein for comments that have improved various incarnations of this review. I am grateful to C. Baskin, F. S. Chapin III, P. Nel, P. B. Tomlinson, C. Vazquez-Yanes, M. Westoby, D. Haig, and especially J. M. Farrant for data, insights, and/or suggestions that have helped these thoughts gel over time. Staff of the Harvard University Herbaria helped immensely with researching seed traits. Research and writing were supported by National Science Foundation grants IBN-9623313 and DGE-9714522 to EJJ, the DeLand Fund of the Arnold Arboretum, and Harvard University.

**Visit the Annual Reviews home page at [www.AnnualReviews.org](http://www.AnnualReviews.org)**

## LITERATURE CITED

1. Ackerly DD, Donoghue MJ. 1998. Leaf size, sapling allometry, and Corner's rules: phylogeny and correlated evolution in maples (*Acer*). *Am. Nat.* 152:767–91
2. Akamine EK. 1951. Viability of Hawaiian forest tree seeds in storage at various temperatures and relative humidities. *Pac. Sci.* 5:36–46
3. Artlip TS, Madison JT, Settler TL. 1995. Water deficit in developing endosperm of maize: cell division and nuclear DNA endoreplication. *Plant Cell Environ.* 18:1034–40
4. Augspurger CK. 1979. Irregular rain cues and the germination and seedling survival of a Panamanian shrub (*Hybanthus prunifolius*). *Oecologia* 44:53–59
5. Auranen M. 1995. Pre-harvest sprouting and dormancy in malting barley in northern climatic conditions. *Acta Agric. Scand.* 45:89–95
6. Ball MC. 1996. Comparative ecophysiology of tropical lowland moist rainforest and mangrove forest. In *Tropical Forest Plant Ecophysiology*, ed. SS Mulkey, RL Chazdon, AP Smith, pp. 461–96. New York: Chapman & Hall
7. Baker HG. 1989. Some aspects of the natural history of seed banks. In *Ecology of Soil Seed Banks*, ed. MA Leck, VT Parker, RL Simpson, pp. 9–21. San Diego, CA: Academic
8. Baker SS, Wilhelm KS, Thomashow MF. 1994. The 5'-region of *Arabidopsis thaliana cor 15a* has cis-acting elements that confer cold-, drought- and ABA-regulated gene expression. *Plant Mol. Biol.* 24:701–13
9. Barton LV. 1961. *Seed Preservation and Longevity*. Plant Sci. Monogr. Ser. New York: InterScience
10. Baskin CC, Baskin JM. 1998. *Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination*. San Diego, CA: Academic
11. Becwar MR, Stanwood PC, Roos ER. 1982. Dehydration effects on imbibitional leakage from desiccation-sensitive seeds. *Plant Physiol.* 69:1132–35
12. Berjak P, Vertucci CW, Pammenter NW. 1992. Homoiohydrous (recalcitrant) seeds: developmental status, desiccation sensitivity and the state of water in axes of *Landolphia kirkii* Dyer. *Planta* 186:249–61

13. Bewley JD. 1997. Seed germination and dormancy. *Plant Cell* 9:1055–66
14. Bewley JD, Black M. 1994. *Seeds: Physiology of Development and Germination*. New York: Plenum
15. Black M, Corbineau F, Grzesik M, Guy P, Come D. 1996. Carbohydrate metabolism in the developing and maturing wheat embryo in relation to its desiccation tolerance. *J. Exp. Bot.* 47:161–69
16. Blom CWPM. 1999. Adaptations to flooding stress: from plant community to molecule. *Plant Biol.* 1:261–73
17. Bonhert HJ, Nelson DE, Jensen RG. 1995. Adaptations to environmental stresses. *Plant Cell* 7:1099–111
18. Bradford KJ, Chandler PM. 1992. Expression of “dehydrin-like” proteins in embryos and seedlings of *Zizania palustris* and *Oryza sativa* during dehydration. *Plant Physiol.* 99:488–94
19. Bray EA. 1997. Plant responses to water deficit. *Trends Plant Sci.* 2:48–54
20. Brenner ML, Cheikh N. 1995. The role of hormones in photosynthate partitioning and seed filling. In *Plant Hormones: Physiology, Biochemistry and Molecular Biology*, ed. PJ Davies, pp. 649–70. Dordrecht, The Netherlands: Kluwer Academic
21. Burggren WW, Bemis WE. 1990. Studying physiological evolution: paradigms and pitfalls. In *Evolutionary Innovations*, ed. MH Nitecki, pp. 191–228. Chicago, IL: Univ. Chicago Press
22. Burrows CJ. 1995. The seeds always know best. *NZ J. Bot.* 32:349–63
23. Burrows CJ. 1996. Germination behavior of the seeds of seven New Zealand vine species. *NZ J. Bot.* 34:93–102
24. Chapin FS III. 1991. Integrated responses of plants to stress. *BioScience* 41:29–36
25. Chapin FS III, Autumn K, Pugnaire F. 1993. Evolution of suites of traits in response to environmental stress. *Am. Nat.* 142 (Suppl.):S78–92
26. Chase MW, Duvall MR, Hills HG, Conran JG, Cox AV, et al. 1995. Molecular phylogenetics of Liliaceae. In *Monocotyledons: Systematics and Evolution*, ed. PJ Rudall, PB Cribb, DF Cutler, CJ Humphries, pp. 109–37. London: R. Bot. Gard. Kew
27. Chiang HH, Dandekar AM. 1995. Regulation of proline accumulation in *Arabidopsis thaliana* (L.) Heynh. during development and in response to desiccation. *Plant Cell Environ.* 18:1280–90
28. Chin HF, Roberts EH. 1980. *Recalcitrant Crop Seeds*. Kuala Lumpur, Malaysia: Tropical
29. Chraïbi A, Palms B, Druart N, Goupil P, Gojon A, et al. 1995. Influence of abscisic acid on nitrogen partitioning, sucrose metabolism and nitrate reductase activity of chicory suspension cells. *J. Exp. Bot.* 46:1525–33
30. Close TJ. 1996. Dehydrins: emergence of a biochemical role of a family of plant dehydration proteins. *Physiol. Plant.* 97:795–803
31. Cohn MA. 1996. Operational and philosophical decisions in seed dormancy research. *Seed Sci. Res.* 6:147–53
32. Cooke T. 1907. The embryology of *Rhizophora mangle*. *Bull. Torrey Bot. Club* 34:271–77
33. Corner EJH. 1976. *The Seeds of Dicotyledons*. Cambridge, UK: Cambridge Univ. Press
34. Cramer GR, Jones RL. 1996. Osmotic stress and abscisic acid reduce cytosolic calcium activities in roots of *Arabidopsis thaliana*. *Plant Cell Environ.* 19:1291–98
35. Crowe JH, Hoekstra FJ, Crowe LM. 1992. Anhydrobiosis. *Annu. Rev. Physiol.* 54:579–99
36. Davies PJ, ed. 1995. *Plant Hormones: Physiology, Biochemistry and Molecular Biology*. Dordrecht, The Netherlands: Kluwer Academic
37. Dodd MC, van Staden J. 1981. Germination and viability studies on the seeds of *Podocarpus henkelii* Stapf. *S. Afr. J. Sci.* 77:171–74
38. Ducker SC, Knox RB. 1976. Submarine

- pollination in sea grasses. *Nature* 263:705–6
39. Dure LS III. 1993. The lea proteins of higher plants. In *Control of Plant Gene Expression*, ed. DPS Verma, pp. 325–35. Boca Raton, FL: CRC Press
40. Ellis RH, Hong TD, Roberts EH. 1985. *Handbook of Seed Technology for Genebanks*. Vol. II, *Compendium of Specific Germination Information and Test Recommendations*. Rome, Italy: Int. Board Plant Genet. Resour.
41. Ellison AM, Farnsworth EJ. 1993. Seedling survivorship, growth and response to disturbance in Belizean mangal. *Am. J. Bot.* 80:1137–45
42. Elmqvist T, Cox PA. 1996. The evolution of vivipary in flowering plants. *Oikos* 77:3–9
43. Elotmani M, Lovatt CJ, Coggins CW, Agusti M. 1995. Plant growth regulators in citriculture: factors regulating endogenous levels in citrus tissues. *Crit. Rev. Plant Sci.* 14:367–412
44. Espelund M, Debedout JA, Outlaw WH, Jakobsen KA. 1995. Environmental and hormonal regulation of barley late-embryogenesis-abundant (Lea) mRNAs is via different signal transduction pathways. *Plant Cell Environ.* 18:943–49
45. Evans AS, Cabin RJ. 1995. Can dormancy affect the evolution of post-germination traits? The case of *Lesquerella fendleri*. *Ecology* 76:344–56
46. Farnsworth EJ. 1997. Evolutionary and Ecological Physiology of Mangrove Seedlings: Correlates, Costs, and Consequences of Viviparous Reproduction. PhD thesis, Harvard Univ., Cambridge, MA. 308 pp.
47. Farnsworth EJ, Ellison AM. 1996. Sunshade adaptability of the red mangrove, *Rhizophora mangle* (Rhizophoraceae): changes through ontogeny at several levels of biological organization. *Am. J. Bot.* 83:1131–43
48. Farnsworth EJ, Ellison AM. 1997. Global patterns of pre-dispersal seed predation in mangrove forests. *Biotropica* 29:318–30
49. Farnsworth EJ, Farrant JM. 1998. Reductions in abscisic acid are linked with viviparous reproduction in mangroves. *Am. J. Bot.* 85:760–69
50. Farrant JM, Pammenter NW, Berjak P. 1989. Germination-associated events and the desiccation sensitivity of recalcitrant seeds: a study on three unrelated species. *Planta* 178:189–98
51. Farrant JM, Pammenter NW, Berjak P. 1993. Seed development in relation to desiccation tolerance: a comparison between desiccation-sensitive (recalcitrant) seeds of *Avicennia marina* and desiccation-tolerant types. *Seed Sci. Res.* 3:1–13
52. Farrant JM, Pammenter NW, Berjak P, Farnsworth EJ, Vertucci CW. 1996. Presence of dehydrin-like proteins and levels of abscisic acid in recalcitrant (desiccation sensitive) seeds may be related to habitat. *Seed Sci. Res.* 6:175–82
53. Farrant JM, Pammenter NW, Cutting JGM, Berjak P. 1993. The role of plant growth regulators in the development and germination of the desiccation-sensitive (recalcitrant) seeds of *Avicennia marina*. *Seed Sci. Res.* 3:55–63
54. Fennimore SA, Foley ME. 1998. Genetic and physiological evidence for the role of gibberellic acid in the germination of dormant *Avena fatua* seeds. *J. Exp. Bot.* 49:89–94
55. Fernandez H, Dumas P, Bonnet-Masimbert M. 1997. Quantification of GA1, GA3, GA4, GA7, GA8, GA9, GA19, and GA20: and GA20 metabolism in dormant and non-dormant beechnuts. *Plant Growth Regul.* 22:29–35
56. Finch CE, Rose MR. 1995. Hormones and the physiological architecture of life history evolution. *Q. Rev. Biol.* 70:1–52
57. Finch-Savage WE. 1992. Seed development in the recalcitrant species *Quercus robur* L.: germinability and desiccation tolerance. *Seed Sci. Res.* 2:17–22
58. Finch-Savage WE, Clay HA. 1994.

- Evidence that ethylene, light and abscisic acid interact to inhibit germination in the recalcitrant seeds of *Quercus robur* L. *J. Exp. Bot.* 45:1295–99
59. Finch-Savage WE, Pramanik SK, Bewley JD. 1994. The expression of dehydrin proteins in desiccation-sensitive (recalcitrant) seeds of temperate trees. *Planta* 193:478–85
60. Finkelstein RR. 1993. Abscisic acid-insensitive mutations provide evidence for stage-specific signal pathways regulating expression of an *Arabidopsis* late embryogenesis-abundant (*Lea*) gene. *Mol. Gen. Genet.* 238:401–8
61. Foster SA. 1986. On the adaptive value of large seeds for moist tropical forest trees: a review and synthesis. *Bot. Rev.* 52:260–99
62. French JC, Chung MG, Hur YK. 1995. Chloroplast DNA phylogeny of the Ariflorae. In *Monocotyledons: Systematics and Evolution*, ed. PJ Rudall, PB Cribb, DF Cutler, CJ Humphries, pp. 255–75. London: R. Bot. Gard. Kew
63. Galau GA, Jakobsen KS, Hughes DW. 1991. The controls of late dicot embryogenesis and early germination. *Physiol. Plant.* 81:280–88
64. Garcia AB, de Almeida Engler J, Claes B, Vuillarroel R, Montagu M, van Gerats T, Caplan A. 1998. The expression of the salt-response gene salt from rice is regulated by hormonal and developmental cues. *Planta* 207:172–80
65. Garello G, LePaige-Degivry MT. 1995. Desiccation-sensitive *Hopea odorata* seeds: sensitivity to abscisic acid, water potential, and inhibitors of gibberellin biosynthesis. *Physiol. Plant.* 95:45–50
66. Garrard A. 1955. The germination and longevity of seeds in an equatorial climate. *Gard. Bull. Singapore* 14:534–45
67. Garwood NC. 1983. Seed germination in a seasonal tropical forest in Panama: a community study. *Ecol. Monogr.* 53:159–81
68. Goebel KE. 1905. *Organography of Plants*. New York: Hafner
69. Grill E, Himmelbach A. 1998. ABA signal transduction. *Curr. Opin. Plant Biol.* 1:412–18
70. Gul B, Weber DJ. 1998. Effect of dormancy-relieving compounds on the seed germination of non-dormant *Allenrolfea occidentalis* under salinity stress. *Ann. Bot.* 82:555–60
71. Guppy HB. 1906. *Observations of a Naturalist in the Pacific Between 1896 and 1899*. Vol. 2, *Plant Dispersal*. London: Macmillan
72. Haberlandt G. 1895. Über die Ernährung der Keimlinge und die Bedeutung des Endosperms bei viviparen Mangrovepflanzen. *Ann. Jard. Bot. Buitenzorg* 12:102–5
73. Hairston NG Jr, Van Brunt RA, Kearns CM, Engstrom DR. 1995. Age and survivorship of diapausing eggs in a sediment egg bank. *Ecology* 76:1706–11
74. Hanelt P. 1977. Okologische und systematische Aspekte der Lebensdauer von Samen. *Biol. Rundsch.* 15:81–91
75. Harper JL, Lovell PH, Moore KG. 1970. The shapes and sizes of seeds. *Annu. Rev. Ecol. Syst.* 1:327–56
76. Harrington JF. 1972. Seed storage and longevity. In *Seed Biology*, Vol. III, ed. TT Kozlowski, pp. 145–250. New York: Academic
77. Hendry GAF. 1993. Oxygen free radical processes and seed longevity. *Seed Sci. Res.* 3:141–53
78. Hilhorst HWM. 1995. A critical update on seed dormancy. *Seed Sci. Res.* 5:61–73
79. Hoekstra FA, Haigh AM, Tetteroo FAA, van Roekel T. 1994. Changes in soluble sugars in relation to desiccation tolerance in cauliflower seeds. *Seed Sci. Res.* 4:143–47
80. Holdsworth M, Kurup S, McKibbin R. 1999. Molecular and genetic mechanisms regulating the transition from embryo development to germination. *Trends Plant Sci.* 4:275–80
81. Hole DJ, Smith JD, Cobb BG. 1989.

- Regulation of embryo dormancy by manipulation of abscisic acid in kernels and associated cob tissue of *Zea mays* L. cultured in vitro. *Plant Physiol.* 91:101–5
82. Hong TD, Ellis RH. 1990. A comparison of maturation drying, germination, and desiccation tolerance between developing seeds of *Acer psuedoplatanus* L. and *Acer platanoides* L. *New Phytol.* 116:589–96
  83. Huttly AK, Phillips AL. 1995. Gibberellin-regulated plant genes. *Physiol. Plant.* 95:310–17
  84. Ingram J, Bartels D. 1996. The molecular basis of dehydration tolerance in plants. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 47:377–403
  85. Janzen DH. 1978. Seeding patterns of tropical forest trees. In *Tropical Trees as Living Systems*, ed. PB Tomlinson, MH Zimmerman, pp. 83–128. Cambridge, UK: Cambridge Univ. Press
  86. Janzen DH. 1983. Costa Rican Natural History. Chicago, IL: Univ. Chicago Press
  87. Jiménez JA. 1994. *Los manglares del Pacífico de Centroamérica*. Heredia, Costa Rica: EFUNA
  88. Johnson-Flanagan AM, Spencer MS. 1994. Ethylene production during development of mustard (*Brassica juncea*) and canola (*Brassica napus*) seed. *Plant Physiol.* 106:601–6
  89. Joshi AC. 1933. A suggested explanation for the prevalence of vivipary on the seashore. *J. Ecol.* 21:209–12
  90. Joshi GV, Jamale BB, Bhosale L. 1975. Ion regulation in mangroves. *Proc. Int. Symp. Biol. Manage. Mangroves*, Vol. 2, ed. GE Walsh, SC Snedaker, HJ Teas, pp. 595–607. Gainesville: Univ. Florida Press
  91. Juncosa AM. 1982. *Embryo and Seedling Development in the Rhizophoraceae*. PhD thesis, Duke Univ., Durham, NC
  92. Juncosa AM, Tomlinson PB. 1988. Systematic comparison and some biological characteristics of Rhizophoraceae and Anisophyllaceae. *Ann. Mo. Bot. Gard.* 75:1296–319
  93. Kawakami K, Miyake Y, Noda K. 1997. ABA insensitivity and low ABA levels during seed development of non-dormant wheat mutants. *J. Exp. Bot.* 48:1415–21
  94. Kepczynski J, Kepczynska E. 1997. Ethylene in seed dormancy and germination. *Physiol. Plant.* 101:720–26
  95. Kermode AR. 1990. Regulatory mechanisms involved in the transition from seed development to germination. *Crit. Rev. Plant Sci.* 9:155–95
  96. Khan AA. 1994. Induction of dormancy in non-dormant seeds. *J. Am. Hort. Soc.* 119:408–13
  97. Kigel J, Galili G. 1995. *Seed Development and Germination*. New York: Marcel Dekker
  98. King J. 1991. *The Genetic Basis of Plant Physiological Processes*. Oxford, UK: Oxford Univ. Press
  99. Kipp-Goller A. 1940. Über Bau und Emtwicklung der viviparen Mangrovekeimlinge. *Z. Bot.* 35:1–40
  100. Knight CD, Sehgal A, Atwal K, Wallace JC, Cove DJ, et al. 1995. Molecular responses to abscisic acid and stress are conserved between moss and cereals. *Plant Cell* 7:499–506
  101. Koornneef M, Rueling G, Karssen CM. 1984. The isolation and characterization of abscisic acid-insensitive mutants of *Arabidopsis thaliana*. *Physiol. Plant.* 61:377–83
  102. Koster KL, Leopold AC. 1988. Sugars and desiccation tolerance in seeds. *Plant Physiol.* 88:829–32
  103. Lalonde J, Saini HS. 1992. Comparative requirement for endogenous ethylene during seed germination. *Ann. Bot.* 69:423–28
  104. Leck MA, Parker VT, Simpson RL, eds. 1989. *Ecology of Soil Seed Banks*. San Diego, CA: Academic
  105. Leite AMC, Rankin JM. 1981. Ecologia de sementes de *Pithecelobium racemosum* Ducke. *Acta Amaz.* 11:309–18
  106. Léon-Kloosterziel KM, Gil MA, Ruijs J,

- Jacobsen SE, Olszewski NE, et al. 1996. Isolation and characterization of abscisic acid-deficient *Arabidopsis* mutants at two new loci. *Plant J.* 10:655–61
107. Léon-Kloosterziel KM, van de Bunt GA, Zeevaart JAD, Koornneef M. 1996. *Arabidopsis* mutants with a reduced seed dormancy. *Plant Physiol.* 110:233–40
108. LePrince O, Bronchart R, Deltour R. 1990. Changes in starch and soluble sugars in relation to the acquisition of desiccation tolerance during maturation of *Brassica campestris* seed. *Plant Cell Environ.* 13:539–46
109. Leung J, Giraudat J. 1998. Abscisic acid signal transduction. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 49:199–222
110. Levin SA, Cohen D, Hastings A. 1984. Dispersal strategies in patchy environments. *Theor. Popul. Biol.* 26:165–91
111. Lin G, da SL Sternberg L. 1995. Variation in propagule mass and its effect on carbon assimilation and seedling growth of red mangrove (*Rhizophora mangle*) in Florida, USA. *J. Trop. Ecol.* 11:109–19
112. Lin TP, Chen MH. 1995. Biochemical characteristics associated with the development of the desiccation-sensitive seeds of *Machilus thunbergii* Sieb and Zucc. *Ann. Bot.* 76:381–87
113. MacIntyre GI. 1987. The role of water in the regulation of plant development. *Can. J. Bot.* 65:1287–98
114. MacNae W. 1968. A general account of the flora and fauna of mangrove swamps and forests in the Indo-West Pacific region. *Adv. Mar. Biol.* 6:73–70
115. Manokoran N. 1978. Germination of fresh seeds of Malaysian rattans. *Malay. For.* 41:319–24
116. Mao ZY, Paiva R, Kriz AL, Juvik JA. 1995. Dehydrin gene expression in normal and viviparous embryos of *Zea mays* during seed development and germination. *Plant Physiol. Biochem.* 33:649–53
117. Marcotte WR Jr, Bayley CC, Quatrano RS. 1988. Regulation of a wheat promoter by abscisic acid in rice protoplasts. *Nature* 335:454–57
118. Marrero J. 1942. A seed storage study of *Maga*. *Caribb. For.* 3:173–84
119. McCarty DR. 1995. Genetic control and integration of maturation and germination pathways in seed development. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 46:71–93
120. McCormick JF. 1995. A review of the population dynamics of selected tree species in the Luquillo experimental forest, Puerto Rico. In *Tropical Forests: Management and Ecology*, ed. AE Lugo, C Lowe, pp. 224–57. New York: Springer-Verlag
121. Meurs C, Basra AS, Karssen CM, van Loon LC. 1992. Role of abscisic acid in the induction of desiccation tolerance in developing seeds of *Arabidopsis thaliana*. *Plant Physiol.* 98:1484–93
122. Mori T, Rahman ZBHA, Tan CH. 1980. Germination and storage of rattan (*Calamus manan*) seeds. *Malay. For.* 43:14–55
123. Mousseau TA, Fox CW. 1998. The adaptive significance of maternal effects. *TREE* 13:403–7
124. Muenscher WC. 1936. Storage and germination of seeds of aquatic plants. *Cornell Univ. Agric. Exp. Stn. Bull.* 642, Cornell Univ., Ithaca, NY
125. Musatenko LI, Berestetsky VA, Vedenicheva NP, Generalova VN, Martyn GI, Sytnik KM. 1995. Phytohormones and structure of cell of *Acer saccharinum* seed embryo. *Biol. Plant.* 37:553–59
126. Ng FSP. 1992. *Manual of Forest Fruits, Seeds and Seedlings*. Kuala Lumpur: For. Res. Inst. Malaysia
127. Nkang A, Chandler G. 1986. Changes during embryogenesis in rainforest seeds with orthodox and recalcitrant viability characteristics. *J. Plant Physiol.* 126:243–56
128. Oliveira LMQ, Valio IFM. 1992. Effects of moisture content on germination

- of seeds of *Hancornia speciosa* Gom. (Apocynaceae). *Ann. Bot.* 69:1–5
129. Oliver MJ, Bewley JD 1997. Desiccation-tolerance of plant tissues: a mechanistic overview. *Hort. Rev.* 18:171–213
  130. Olmstead RG, Bremer B., Scott KM, Pamer JD. 1993. A parsimony analysis of the Asteridae *sensu lato* based on *rbcL* sequences. *Ann. Mo. Bot. Gard.* 80:700–22
  131. Osborne DJ, Boubriak II. 1994. DNA and desiccation tolerance. *Seed Sci. Res.* 4:175–85
  132. Pammenter NW, Berjak P, Farrant JM, Smith MT, Ross G. 1994. Why do stored hydrated recalcitrant seeds die? *Seed Sci. Res.* 4:187–91
  133. Pannier RF, Pannier F. 1973. Determinación de substancias de tipo gibberellina en tejidas de *Rhizophora mangle* en diferentes etapas de desarrollo. *Acta Cient. Venez.* 24(Suppl. 1):33–34
  134. Paz H, Mazer SJ, Martínez-Ramos M. 1999. Seed mass, seedling emergence, and environmental factors in seven rain forest *Psychotria* (Rubiaceae). *Ecology* 80:1594–606
  135. Pence VC. 1991. Abscisic acid in developing zygotic embryos of *Theobroma cacao*. *Plant Physiol.* 95:1291–93
  136. Peroni PA. 1995. Field and laboratory investigations of seed dormancy in red maple (*Acer rubrum* L.) from the North Carolina piedmont. *For. Sci.* 41:378–86
  137. Philbrick CT, Les DH. 1996. Evolution of aquatic angiosperm reproductive systems. *BioScience* 46:813–26
  138. Popp M. 1995. Salt resistance in herbaceous halophytes and mangroves. *Prog. Bot.* 56:416–42
  139. Pritchard HW, Tompsett PB, Manger KR. 1996. Development of a thermal time model for the quantification of dormancy loss in *Aesculus hippocastaneum* seeds. *Seed Sci. Res.* 6:127–35
  140. Probert RJ, Longley PL. 1989. Recalcitrant seed storage physiology in three aquatic grasses (*Zizania palustris*, *Spartina anglicaa* and *Porteresia coarctata*). *Ann. Bot.* 63:53–63
  141. Pronzato R, Manconi R. 1994. Life history of *Ephydatia fluviatilis*: a model for adaptive strategies in discontinuous habitats. In *Sponges in Time and Space, Proc. Int. Porifera Congr., 4th*, ed. RWM van Soest, 327–34. Rotterdam, The Netherlands: Balkema
  142. Puchet CE, Vazquez-Yanes C. 1987. Heteromorfismo criptico en las semillas recalcitrantes de tres especies de la selva tropical humeda de Veracruz, Mexico. *Phytologia* 62:100–6
  143. Ravishankar KV, Shaanker RU, Ganeshiah KN. 1995. War of hormones over resource allocation to seeds: strategies and counter-strategies of offspring and maternal parent. *J. Biosci.* 20:89–103
  144. Rees M. 1994. Delayed germination of seeds: a look at the effects of adult longevity, the timing of reproduction, and population age/stage structure. *Am. Nat.* 144:43–64
  145. Ringlund K, Mosleth E, Mares DJ, eds. 1990. *Fifth International Symposium on Pre-harvest Sprouting in Cereals*. Boulder, CO: Westview
  146. Roberts EH. 1973. Predicting the storage life of seeds. *Seed Sci. Technol.* 1:499–514
  147. Robertson, AI, Giddens R, Smith TJ III. 1990. Seed predation by insects in tropical mangrove forests: extent and effects on seed viability and the growth of seedlings. *Oecologia* 83:213–19
  148. Rock CD, Quatrano RS. 1995. The role of hormones during seed development. In *Plant Hormones: Physiology, Biochemistry and Molecular Biology*, ed. PJ Davies, pp. 671–697. Dordrecht, The Netherlands: Kluwer Academic
  149. Romagosa I, Han F, Clancy JA, Ulrich SE. 1999. Individual locus effects on dormancy during seed development and after ripening in barley. *Crop Sci.* 39:74–79

150. Schachtman D, Liu W. 1999. Molecular pieces to the puzzle of the interaction between potassium and sodium uptake in plants. *Trends Plant Sci.* 4:281–87
151. Schupp EW. 1995. Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. *Am. J. Bot.* 82:399–409
152. Setoguchi H, Kosuge K, Tobe H. 1999. Molecular phylogeny of Rhizophoraceae based on *rbcL* gene sequences. *J. Plant Res.* 112:443–55
153. Sheen J. 1996. Ca<sup>2+</sup>-dependent protein kinases and stress signal transduction in plants. *Science* 274:1900–2
154. Silvertown JW. 1981. Seed size, life span, and germination date as co-adapted features of plant life history. *Am. Nat.* 118:860–64
155. Skriver K, Mundy J. 1990. Gene expression in response to abscisic acid and osmotic stress. *Plant Cell* 2:503–12
156. Smirnoff N. 1993. The role of active oxygen in the response of plants to water deficit and desiccation. Tansley Review 52. *New Phytol.* 125:27–58
157. Smith SM, Snedaker SC. 1995. Salinity responses in two populations of viviparous *Rhizophora mangle* L. seedlings. *Biotropica* 27:435–40
158. Smith-Ramirez C, Armesto JJ, Figueroa J. 1998. Flowering, fruiting and seed germination in Chilean rain forest Myrtaceae: ecological and phylogenetic constraints. *Plant Ecol.* 136:119–31
159. Smythe M. 1970. Relationships between fruiting seasons and seed dispersal methods in a neotropical forest. *Am. Nat.* 104:25–35
160. Stearns SC, Schmid-Hempel P. 1987. Evolutionary insights should not be wasted. *Oikos* 49:118–25
161. Steinbach HS, Benecharnold RL, Kristof G, Sanchez RA, Marcuccipoltri S. 1995. Physiological basis of pre-harvest sprouting resistance in *Sorghum bicolor* (L.) Moench. ABA levels and sensitivity in developing embryos of sprouting-resistant and sprouting-susceptible varieties. *J. Exp. Bot.* 46:701–9
162. Stöcklin J, Fischer M. 1999. Plants with longer-lived seeds have lower local extinction rates in grassland remnants 1950–1985. *Oecologia* 120:539–43
163. Sussex I. 1975. Growth and metabolism of the embryo and attached seedling of the viviparous mangrove, *Rhizophora mangle*. *Am. J. Bot.* 62:948–53
164. Swamy BGL, Padmanabhan D. 1961. Nutulae embryologieae. I. The functions of endosperm in *Avicennia officinalis*. *Curr. Sci.* 30:424–25
165. Takahashi N, Phinney BO, MacMillan J, eds. 1991. *Gibberellins*. Berlin: Springer-Verlag
166. Takhtajan A. 1991. *Evolutionary Trends in Flowering Plants*. New York: Columbia Univ. Press
167. Tan H, Rao AN. 1981. Vivipary in *Ophiorrhiza tomentosa* Jack (Rubiaceae). *Biotropica* 13:232–33
168. Tetteroo FAA, Bomal C, Hoekstra FA, Karssen CM. 1994. Effect of abscisic acid and slow drying on soluble carbohydrate content in developing embryoids of carrot (*Daucus carota* L.) and alfalfa (*Medicago sativa* L.). *Seed Sci. Res.* 4:203–10
169. Thomas TH, Hare PD, Van Staden J. 1997. Phytochrome and cytokinin responses. *Plant Growth Regul.* 23:105–22
170. Thompson K. 1987. Seeds and seed banks. *New Phytol.* 106:23–34
171. Thompson K, Bakker JP, Bekker RM, Hodgson JG. 1998. Ecological correlates of seed persistence in soil in the north-west European flora. *J. Ecol.* 86:163–69
172. Thornton TM, Swain SM, Olszewski NE. 1999. Gibberellin signal transduction presents... the SPY who O-GlcNAc'd me. *Trends Plant Sci.* 4:424–28
173. Tomlinson PB. 1986. *The Botany of Mangroves*. Cambridge, UK: Cambridge Univ. Press
174. Tompsett PB. 1982. The effect of desiccation on the longevity of seeds of

- Araucaria hunsteinii* and *A. cunninghamii*. *Ann. Bot.* 50:693–704
175. Tompsett PB, Pritchard HW. 1998. The effect of chilling and moisture status on the germination, desiccation tolerance and longevity of *Aesculus hippocastanum* L. seed. *Ann. Bot.* 82:249–61
  176. Trethowan RM, Rajaram S, Ellison FW. 1996. Pre-harvest sprouting tolerance of wheat in the field and under rain simulation. *Aust. J. Agric. Res.* 47:705–16
  177. Trewavas A J. 1987. Sensitivity and sensory adaptation in growth substance responses. In *Hormone Action in Plant Development*, ed. GV Hoad, MB Jackson, JR Lenton, RK Atkin, pp. 19–38. London: Butterworth
  178. Treub M. 1883. Notes sur l'embryon: le sac embryonnaire et l'ovule *Avicennia officinalis*. *Ann. Jard. Bot. Buitenzorg* 3:79–85
  179. Uhl NW, Dransfield J, Davis JI, Luckow MA, Hansen KS, Doyle JJ. 1995. Phylogenetic relationships among palms: cladistic analyses of morphological and chloroplast DNA restriction site variation. In *Monocotyledons: Systematics and Evolution*, ed. PJ Rudall, PB Cribb, DF Cutler, CJ Humphries, pp. 623–61. London: R. Bot. Gard. Kew
  180. Ungar IA. 1991. *Ecophysiology of Halophytes*. Boca Raton, FL: CRC Press. 209 pp.
  181. van der Pijl L. 1983. *Principles of Dispersal in Higher Plants*. Berlin: Springer-Verlag
  182. VanDuijn B, Flikweert MT, Heidekamp F, Wang M. 1996. Different properties of the inward rectifying potassium conductance of aleurone protoplasts from dormant and non-dormant barley grains. *Plant Growth Regul.* 18:107–13
  183. Vartanian N. 1996. Mutants as tools to understand cellular and molecular drought tolerance mechanisms. *Plant Growth Regul.* 20:125–34
  184. Vazquez-Yanes C, Arechiga MR. 1996. Ex situ conservation of tropical rain forest seed: problems and perspectives. *Interciencia* 21:293
  185. Vazquez-Yanes C, Orozco Segovia A. 1984. Ecophysiology of seed germination in the tropical humid forests of the world: a review. In *Physiological Ecology of Plants in the Wet Tropics*, ed. E Medina, HA Mooney, C Vazquez-Yanes, pp. 37–50. The Hague: Junk
  186. Venable DL, Brown JS. 1988. The selective interactions of dispersal, dormancy and seed size as adaptations for reducing risk in variable environments. *Am. Nat.* 131:360–84
  187. Vertucci CW, Farrant JM. 1995. Acquisition and loss of desiccation tolerance. In *Seed Development and Germination*, ed. J Kigel, G Galili, pp. 237–71. New York: Marcel Dekker
  188. Vleeshouwers LM, Bouwmeester HJ, Karssen CM. 1995. Redefining seed dormancy: an attempt to integrate physiology and ecology. *J. Ecol.* 83:1031–37
  189. Voeseek LACJ, Blom CWPM. 1996. Plants and hormones: an ecophysiological view on timing and plasticity. *J. Ecol.* 84:111–19
  190. von Teichman I, van Wyk AE. 1991. Trends in the evolution of dicotyledonous seeds based on character associations, with special reference to pachychalazy and recalcitrance. *Bot. J. Linn. Soc.* 105:211–37
  191. von Teichman I, van Wyk AE. 1994. Structural aspects and trends in the evolution of recalcitrant seeds in dicotyledons. *Seed Sci. Res.* 4:225–39
  192. Walker-Simmons M. 1988. ABA levels and sensitivity in developing wheat embryos of sprouting resistant and susceptible cultivars. *Plant Physiol.* 84:61–66
  193. Walter H, Steiner M. 1936. Die Oekologie der Ostafrikanischen Mangroven. *Z. Bot.* 30:65–193
  194. Ward JM, Pei Z-M, Schroeder JI. 1995. Roles of ion channels in initiation of

- signal transduction in higher plants. *Plant Cell* 7:833–44
195. Webb AAR, McAinsh MR, Taylor JE, Hetherington AM. 1996. Calcium ions as intracellular second messengers in higher plants. *Adv. Bot. Res.* 22:45–96
196. Weber H, Borisjuk L, Wobus U. 1997. Sugar import and metabolism during seed development. *Trends Plant Sci.* 2:169–74
197. Weyers JDB, Peterson NW, Abrook R, Peng ZY. 1995. Quantitative analysis of the control of physiological phenomena by plant hormones. *Physiol. Plant.* 95:486–94
198. Willson MF. 1983. *Plant Reproductive Ecology*. New York: Wiley & Sons
199. Wise RR, Juncosa AM. 1989. Ultrastructure of the transfer tissues during viviparous seedling development in *Rhizophora mangle* (Rhizophoraceae). *Am. J. Bot.* 76:1286–98
200. Xu NF, Bewley JD. 1995. The role of abscisic acid in germination, storage protein synthesis and desiccation-tolerance in alfalfa (*Medicago sativa* L.) seeds, as shown by inhibition of its synthesis by fluridone during development. *J. Exp. Bot.* 46:687–94
201. Young JA, Young CG. 1992. *Seeds of Woody Plants of North America*. Portland, OR: Dioscorides
202. Zhang J, Davies WJ. 1989. Abscisic acid produced in dehydrating roots may enable the plant to measure the water status of the soil. *Plant Cell Environ.* 12:73–81
203. Zheng WJ, Wang WQ, Lin P. 1999. Dynamics of element contents during the development of hypocotyles and leaves of certain mangrove species. *J. Exp. Mar. Biol. Ecol.* 233:247–57