THE ECOLOGY AND PHYSIOLOGY OF VIVIPAROUS AND RECALCITRANT SEEDS

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■ **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,

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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

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

(*Continued*)

TABLE 1 *(Continued)*

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

(Continued)

TABLE 1 *(Continued)*

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

(Continued)

TABLE 1 (*Continued*)

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

[a]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") of 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

MBRYO 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

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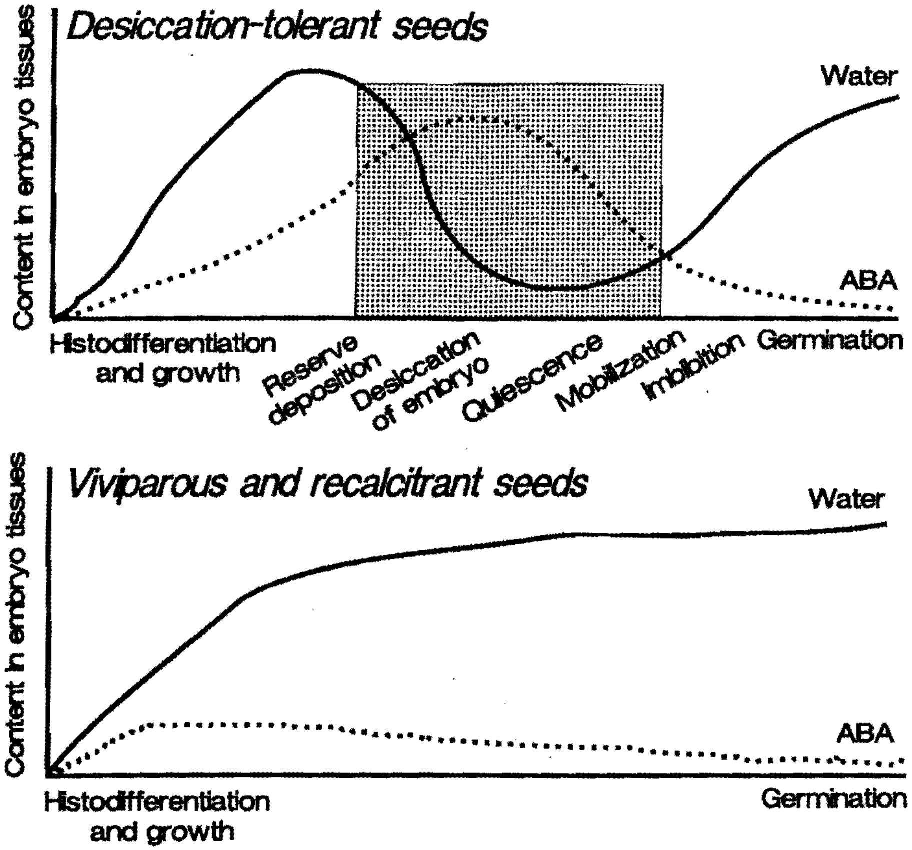

Figure 1 A graphical comparison of the dynamics of water and abscisic acid (ABA) in recalcitrant and viviparous (desiccation-intolerant) and dormant (desiccation-tolerant) seeds. Recalcitrant and viviparous embryos cannot dry, and they do not enter a dormant phase. Desiccation-tolerant embryos, by contrast, 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.

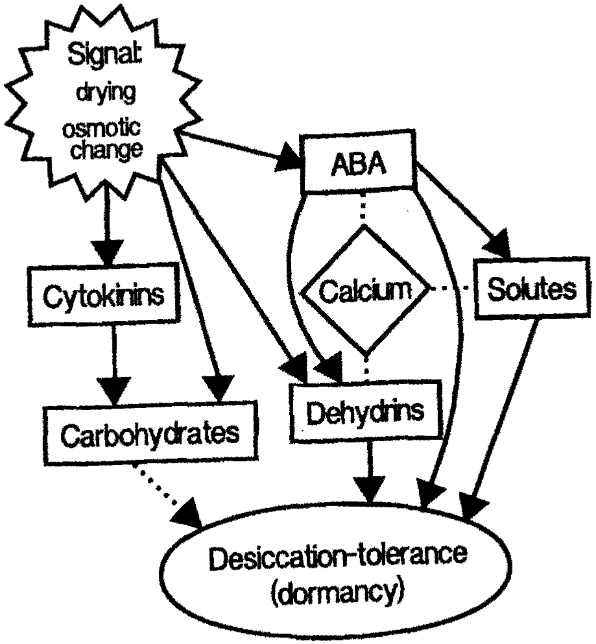

Figure 2 Linkages among multiple pathways for regulating desiccation tolerance in plant tissues, including seeds. An environmental signal that induces a change in osmotic status triggers production of the phytohormone abscisic acid (ABA) and its cofactor, calcium, which in turn transduces signals for 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 (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

Structure	Cytokinins	Auxin	Gibberellins	Abscisic acid	Ethylene
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 cotyledon 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; increase 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 climes (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).

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 wh organism levels.

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