

Seed dormancy in trees of climax tropical vegetation types

CAROL C. BASKIN^{1,2,*} & JERRY M. BASKIN¹

¹*Department of Biology, University of Kentucky, Lexington, KY 40506-0225 USA;* ²*Department of Plant and Soil Science, University of Kentucky, Lexington, KY 40546-0312 USA*

Abstract: This review includes data on classes of seed dormancy, or of nondormancy, for 2040 species of trees in climax tropical forests: evergreen, 1098; semievergreen, 515; deciduous, 133; savanna, 223; and montane, 71. In evergreen, semievergreen, deciduous, savanna, and montane forests, 57.3, 52.0, 34.8, 37.8, and 33.8% of the species, respectively, had nondormant seeds. Overall, there was an increase in dormancy with decreases in temperature and precipitation across the gradient of forest types from evergreen to montane forests, but deciduous, savanna, and montane forests had about the same proportion of species with dormant seeds. Depending on the family, there were increases, decreases, or no change in proportion of species with dormant seeds across the gradient. Considering only the species with dormant seeds, physiological dormancy decreased from evergreen to deciduous forests but increased slightly in savanna and montane forests. On the other hand, physical dormancy increased from evergreen to savanna forests but decreased in the montane. Morphological dormancy decreased from evergreen to savanna forests but increased in montane forests. Morphophysiological dormancy decreased from evergreen to deciduous forests but increased in savanna and montane forests. Combinational dormancy (physical + physiological), which never exceeded 2%, was found only in evergreen and montane forests. Much research remains to be done to understand the evolutionary origins and biogeography of seed dormancy in tropical trees, and it is suggested that working on members of plant families that occur across the gradient of forest types may be a rewarding approach.

Resumen: Esta revisión incluye datos sobre los tipos de latencia de las semillas, o de ausencia de latencia, para 2040 especies de árboles en bosques tropicales clímax: perennifolios, 1098; subperennifolios, 515; caducifolios, 133; de sabana, 223; y de montaña, 71. En los bosques perennifolios, subperennifolios, caducifolios, de sabana y de montaña, 57.3, 52.0, 34.8, 37.8, y 33.8% de las especies, respectivamente, tuvieron semillas no latentes. En términos generales, la incidencia de la latencia se incrementó con los decrementos en temperatura y precipitación a través del gradiente de tipos de bosque desde los perennifolios hasta los bosques de montaña, pero los bosques caducifolios, los de sabana y los de montaña tuvieron más o menos la misma proporción de especies con semillas latentes. Dependiendo de la familia, hubo incrementos o decrementos, o incluso no hubo cambios, en la proporción de especies con semillas latentes a través del gradiente. Considerando sólo a las especies con semillas latentes, la latencia fisiológica decreció de los bosques perennifolios a los caducifolios, pero tuvo un ligero incremento en los bosques de sabana y de montaña. Por otra parte, la latencia física se incrementó de los bosques perennifolios a los de sabana, pero decreció en los bosques de montaña. La latencia morfológica decreció de los bosques perennifolios a los de sabana, pero se incrementó hacia los bosques de montaña. La latencia morfofisiológica disminuyó de los bosques perennifolios a los caducifolios, pero aumentó en los bosques de sabana y los de montaña. La latencia combinatoria (física + fisiológica), la cual nunca excedió de 2%, fue

* e-mail: ccbask0@uky.edu

registrada solamente en bosques perennifolios y de montaña. Hace falta mucha investigación para entender los orígenes evolutivos y la biogeografía de la latencia de las semillas en árboles tropicales, y se sugiere que el trabajo con miembros de familias de plantas que estén presentes en todo el gradiente de tipos de bosques puede ser un enfoque provechoso.

Resumo: Esta revisão inclui dados em classes de dormência seminal, ou de não dormência, de 2040 espécies de árvores nas florestas tropicais clímax: sempreverdes, 1098; semi-sempreverdes, 515; decíduas, 133; savana, 223; e montanas, 71. Nas espécies das florestas sempreverdes, semi-sempreverdes, decíduas, de savana e montanas, 57,3, 52,0, 34,8 e 33,8%, respectivamente, as árvores têm sementes sem dormência. No seu conjunto houve um aumento de dormência com o aumento na temperatura e precipitação através do gradiente de tipos florestais do sempreverde ao montano, mas as florestas decíduas, de savana e montanas apresentaram praticamente a mesma proporção de espécies com sementes dormentes. Dependendo da família, houve aumentos, decréscimos, ou não mudança na proporção de espécies com sementes dormentes através do gradiente. Considerando só as espécies com sementes dormentes, a dormência fisiológica decresceu das florestas sempreverdes às florestas decíduas mas aumentou ligeiramente nas florestas de savana e montanas. Por outro lado, verificou-se que a dormência física aumentou das florestas sempreverdes às de savana mas decresceu nas florestas montanas. Quanto à dormência morfológica ela decresceu das florestas sempreverde às de savana mas aumentou nas florestas montanas. Já no que se refere à dormência morfofisiológica ela decresceu das florestas sempreverdes às decíduas mas aumentou para as florestas de savana e montanas. A dormência combinada (física + fisiológica), a qual nunca excedeu 2%, só foi encontrada nas florestas sempreverdes e montanas. Para compreensão da origem evolutiva e a biogeografia da dormência das sementes nas árvores tropicais muita investigação está ainda por fazer, sugerindo-se que trabalhar sobre membros de famílias que ocorrem através dos gradientes de tipos florestais pode ser uma abordagem compensadora.

Key words: climax tropical forest trees, climax tropical forest vegetation, nondormancy of seeds, seed dormancy, seed germination.

Introduction

Information on the dormancy breaking and germination requirements of seeds is critical to understanding not only the population dynamics of a species, but also how to propagate it either *in situ* or *ex situ*. The need to germinate seeds of tropical trees increases each year due to the growing demand from silviculture and restoration efforts in various locations throughout tropical regions of the world (e.g. Engel & Parrotta 2001; Kopachon *et al.* 1996; Nansen *et al.* 2001). Much emphasis has been placed on the fact that seeds of many tropical trees are nondormant (e.g. Casasola 1976), but it has been known for a long time that seed dormancy is present in some species (e.g. Jones 1956; Ng 1973). Recent data compilations revealed that the relative proportion of tropical

species with dormant *vs.* nondormant seeds varies with the vegetation zone (type of forest), and it tends to increase with a decrease in temperature and precipitation as one moves north or south from the equatorial evergreen rainforests (see Fig. 12.1 in Baskin & Baskin 1998).

In this paper, we use the term *dormancy* to mean that seeds (or other germination units) will not germinate under otherwise favorable conditions of temperature, moisture, and light, whereas *nondormant* seeds will germinate over the widest range of conditions possible for the taxon or genotype. We recognize five classes of dormancy: physiological, morphological, morphophysiological, physical, and combinational (physical + physiological), and they now will be summarized briefly (Baskin & Baskin, 1998; Nikolaeva 1969) below. Seeds with *physiological dormancy* do not

germinate because the embryo has a physiological “problem” that results in low growth potential of the embryo, but as dormancy break occurs, growth potential increases to the point that germination is possible. Three levels of physiological dormancy are recognized: deep, intermediate, and nondeep (Nikolaeva 1969). *Morphological dormancy* is due to the presence of a small or underdeveloped embryo that must grow to a species-specific critical length before radicle emergence is possible. Depending on the species, embryos in freshly-matured seeds begin to grow within a period of a few days to 1-2 wk, and seeds germinate within 1 to about 4 wk. Seeds with *morphophysiological dormancy* have underdeveloped embryos that are physiologically dormant; thus, germination does not occur until physiological dormancy has been broken and embryos have grown. *Physical dormancy* is caused by one or more water-impermeable palisade layers in the seed (or fruit) coat, and dormancy break involves disruption of a specialized area of the seed (e.g. lens in Fabaceae) or fruit coat, thereby creating an opening, which is the site of water entry. Seeds with *combinational dormancy* have impermeable seed (or fruit) coats plus physiologically dormant embryos. Thus, in order for the seeds to germinate the coat has to become permeable to water, and the physiological dormancy of the embryo must be broken.

Some information on the occurrence of the various classes of seed dormancy previously has been compiled for a total of 969 species of trees growing in tropical evergreen, semievergreen, deciduous, and savanna forests (see Fig. 12.3 in Baskin & Baskin 1998). However, this is a relatively small sample of the total number of tree species growing in these vegetation types, and montane was not included because data were available for only two species. Since 1998, we have been accumulating additional information on presence *vs.* absence of dormancy in seeds of tropical trees and on class of dormancy for those seeds in which dormancy was present. The present review includes data for 2040 species of trees in climax tropical forests: evergreen, 1098; semievergreen, 515; deciduous, 133; savannas, 223; and montane, 71.

The purpose of our review is to compare tropical evergreen, semievergreen, deciduous, savanna, and montane forests with regard to: (1) proportion of tree species with nondormant *vs.*

dormant seeds in these different forest types, (2) the relative importance of the various classes of dormancy among trees in the different forest types, and (3) the relative importance of the various classes of dormancy within the same family across the gradient of tropical forest types. Knowing the class of dormancy to be found, or at least expected, in seeds within a family (or even in the same genus) one is attempting to germinate is an important step in deciding what dormancy-breaking treatments to use.

Compilation of data on dormancy in tropical trees

Most studies on germination of seeds of climax tropical trees have not been conducted in incubators using a range of controlled temperatures and light:dark conditions; however, there are exceptions (see Arasaki & Felipe 1987; Corbineau & Côme 1988; Corbineau *et al.* 1986; Tambelini & Perez 1999). Many studies have been conducted at room temperatures (Beniwal & Singh 1989; Uniyal & Nautiyal 1998) or at natural (Garcia & Stéfano 1998; Kyereh *et al.* 1999;) or near-natural temperatures, e.g. 27° C (Vieira *et al.* 1996); 30° C (Das & Thapliyal 1999; de Souza *et al.* 1999). Important information on seed germination rates (i.e. time to germination) has come from studies in which seeds were sown out-of-doors, frequently under light shading, and watered regularly (Conrado *et al.* 1993; Garwood 1983; Holmes 1954; Lorenzi 1998; Ng 1973, 1978, 1980; Ng & Asri 1979; Troup 1921). In phenology studies done under natural or near-natural conditions, data on the length of time between sowing and germination can be used to infer whether or not freshly-matured seeds are dormant. Seeds germinating in 4 wk or less are considered nondormant, while those requiring more than about 4 wk are considered dormant (Baskin & Baskin 1998).

Some authors (e.g. Albrecht 1993; Holmes 1954; Msanga 1998; Watkins 1960) have been concerned not only with producing seedlings of tropical trees but also with determining the cause for lack of germination. Thus, their publications provide information on how long seeds can be stored without loss of viability, time to germination, and special treatments (especially for seeds with physical dormancy) required to promote

germination. For many tropical trees with dormant seeds, however, no studies have been done to determine the cause of dormancy. Therefore, if phenology data indicate that seeds are dormant, i.e. germination is delayed for longer than about 4 wk, class of dormancy for the seeds may have to be inferred from knowledge of kind of embryo (*sensu* Martin 1946) and whether or not seed (or fruit) coats are water-impermeable. If the species belongs to a family in which underdeveloped (small) embryos are known to occur (Table 1), one would suspect that dormant seeds have either morphological or morphophysiological dormancy. It should be noted, however, that not every member of each of these families has underdeveloped embryos. For example, some species of *Fraxinus*, in the Oleaceae, have an underdeveloped embryo, while other genera of the family, including *Chionanthus*, *Forestiera*, *Ligustrum*, *Noronhia*, *Olea*, *Osmanthus*, *Schrebera*, *Syringa*, and *Mendora*, have fully developed embryos (Bossert 1973; Martin 1946; Rocas 1988). On the other hand, seeds of the 19 genera of Annonaceae that have been examined for the type of embryo have underdeveloped embryos (Corner 1976; Garwood & Tebbs 1995; Martin 1946; Rocas 1988; Svoma 1997, 1998; Takhtajan 1988). The list in Table 1 may not be complete, and consequently underdeveloped embryos may be identified in other families, especially in tropical regions.

Some members of Anacardiaceae, Bixaceae, Bombacaceae, Cannaceae, Cistaceae, Cochlospermaceae, Convolvulaceae, Cucurbitaceae, Cuscutaceae, Dipterocarpaceae (subfamilies Monotoieae and Pakaraimoideae but not subfamily Dipterocarpoideae), Fabaceae, Geraniaceae, Malvaceae, Nelumbonaceae, Rhamnaceae, Sarcolaenaceae, Sapindaceae, Sterculiaceae, and Tiliaceae have seeds (or fruits) that are impermeable to water, and consequently the dispersal unit has physical dormancy (Baskin *et al.* 2000). According to the APG (1998), the Bombacaceae, Sterculiaceae, and Tiliaceae are now included in the Malvaceae, and Cuscutaceae is part of the Convolvulaceae; however, for ease of handling data reported in the literature we have kept these as separate families. If a member of one of these 19 families has dormant seeds (or fruits), there is a possibility that they have physical dormancy. However, not every member of each of

these 19 families has physical dormancy. For example, in the Anacardiaceae physical dormancy appears to be restricted to the genus *Rhus sensu lato* and closely-related genera such as *Cotinus*, *Toxicodendron*, and *Malosma*, while all the members of some families such as the Cistaceae and Geraniaceae appear to have physical dormancy (Baskin & Baskin 1998). The only way to be sure whether or not seeds (or fruits) are impermeable to water is to do imbibition studies. Seeds that do not imbibe water have physical dormancy (or rarely combinational), and those that do imbibe water have either physiological, morphological, or morphophysiological dormancy.

Table 1. Plant families in which seeds of one to many species have underdeveloped (*i.e.* small but differentiated) embryos and thus show morphological or morphophysiological dormancy (updated from Baskin & Baskin 1998).

Agavaceae	Dilleniaceae*	Olaceaceae*
Alstroemeriaceae	Escalloniaceae	Oleaceae
Amaryllidaceae	Eupomatiaceae	Opiliaceae*
Amborellaceae	Eupteleaceae	Paeoniaceae
Annonaceae*	Fumariaceae	Pandanaceae
Apiaceae	Garryaceae	Papaveraceae
Aquifoliaceae*	Ginkgoaceae	Philydraceae
Araceae	Grossulariaceae	Piperaceae
Araliaceae*	Gunneraceae	Pittosporaceae*
Arecaceae*	Haemodoraceae	Podocarpaceae*
Aristolochiaceae	Herreriaceae	Ranunculaceae
Asteliaceae	Himantandraceae	Santalaceae
Atherospermaceae	Hydrophyllaceae	Sargentodoxaceae
Aucubaceae	Icacinaceae*	Sarraceniaceae
Austrobaileyaceae	Illiciaceae	Schisandraceae
Berberidaceae	Iridaceae	Siparunaceae
Bromeliaceae	Lactoridaceae	Stemonaceae
Buxaceae	Lardizabalaceae	Smilacaceae
Canellaceae*	Liliaceae	Taxaceae
Caprifoliaceae	Loranthaceae	Tetracentraceae
Chloranthaceae	Magnoliaceae*	Thurniaceae
Circaeasteraceae	Meliantaceae	Tremandaceae
Convallariaceae	Menyanthaceae	Trimeniaceae
Cycadaceae	Monimiaceae*	Trochodendraceae
Daphniphyllaceae	Myristicaceae*	Velloziaceae
Degeneriaceae	Nandinaceae	Winteraceae*

* Families in which trees in tropical climax vegetation occur.

In compiling/using data from phenology studies, we have considered seeds dormant if they required longer than 4 wk for germination; this is consistent with Baskin & Baskin (1998). If seeds were nondormant and the species belongs to a family, and especially to a genus, known to have underdeveloped embryos, it was recorded as having morphological dormancy. On the other hand, if seeds were dormant and the species belongs to a family, and especially to a genus, known to have underdeveloped embryos, it was recorded as having morphophysiological dormancy. If seeds were dormant and the species belongs to a family, especially a genus, known to have impermeable seed (or fruit) coats, it was recorded as having physical dormancy. If seeds were dormant, and the species did not belong to a family or genus known to have underdeveloped embryos or impermeable seed (or fruit) coats, it was recorded as having physiological dormancy. The combination of physical and physiological dormancies in seeds was recorded only when experimental evidence for both physical and physiological dormancy was presented.

It is well known that many species of tropical trees have recalcitrant seeds. Thus, if their moisture content drops below a certain species-specific critical level they die (see Table 9.2 in Baskin & Baskin, 1998). Consequently, rapid germination is characteristic of most recalcitrant seeds (Msanga 1998; Ng 1973, 1978; Ng & Asri 1979). Generally, seeds described in the literature as being recalcitrant, e.g. *Trichilia dregenana* (Drew *et al.* 2000), can be considered nondormant, unless they have an underdeveloped embryo, in which they would have morphological dormancy. However, even with recalcitrant seeds, attention needs to be given to time required for germination to occur. For example, although Msanga (1998) described seeds of *Beilschmiedia kweo* (Lauraceae) as being recalcitrant they had germinated to only 12% after 2 mo but to 70% after 3 mo; thus, apparently a high proportion of the seeds had physiological dormancy. Further, seeds of *Garcinia livingstonii* (Clusiaceae) and *Ocotea usambarensis* (Lauraceae) are described as being recalcitrant (Hong *et al.* 1998; Msanga 1998), but germination continued for 7 wk, indicating that at least some seeds of each species had physiological dormancy (Msanga 1998).

Tropical vegetation zones, as recognized by Walter (1979), have been used in categorizing/organizing the information on germination from numerous studies of tropical trees. Further, the vegetation zones, or forest types, have been arranged to reflect the decreases in temperature and precipitation as one moves north or south from the equator (*sensu* Walter 1979). Montane forests have been placed at the coolest and driest end of the environmental gradient, but it should be noted that within this forest type temperature will vary depending on elevation. Further, depending on whether montane forests are on the windward or leeward side of a mountain they could be relatively wet or dry, respectively.

Results of data compilation

Nondormancy vs. dormancy

In evergreen forests, more species had nondormant than dormant seeds, but in semievergreen forests the proportion of species with nondormant and dormant seeds was about equal (Fig. 1a). In deciduous, savanna, and montane forests, however, more species had dormant than nondormant seeds. The proportion of tree species with dormant seeds in deciduous, savanna, and montane forests was very similar, *i.e.* 35%, 38%, and 34%, respectively.

For evergreen forests, 92 families were recorded, and 17 of them did not have a representative with dormant seeds; semievergreen forests, 83 families and 16 with no dormancy; deciduous forests, 29 families and 11 with no dormancy; savannas, 57 families and 10 with no dormancy; and montane, 36 families and 8 with no dormancy (Table 2). To help evaluate the lack of dormancy in these families, we need to look at the number of species recorded for each family in each forest type and determine how many of them had nondormant seeds (Table 2). Although many families are represented by one or more species with nondormant seeds in one or more forest types, they also are well represented by species with dormant seeds in other forest types, e.g. Apocynaceae, Lecythidaceae, Meliaceae, Myrtaceae, Sapindaceae, and Sapotaceae (Table 2). However, the Bignoniaceae and Dipterocarpaceae had only a few species with dormant seeds, and the species with dormant seeds occurred in evergreen forests.

Table 2. Number of species in various families and tropical forest types with nondormant seeds. Number inside parenthesis is total number of species recorded for the family in a forest type.

Family	Forest type				
	Ever-green	Semiever-green	Deci- duous	Sava- nna	Mon- tane
Actinidaceae	1(1)				
Alangiaceae	1(1)				
Apocynaceae ^T	24(32)	7(10)	1(1)		
Araucariaceae	4(4)	0(1)			
Betulaceae ^T			1(1)		1(1)
Bignoniaceae ^T	16(17)	18(18)	1(1)	5(5)	1(1)
Capparidaceae		1(2)		2(2)	
Caricaceae		1(1)			
Casuarinaceae			1(1)		
Convolvulaceae ^T	1(1)				
Dipterocarpaceae	69(71)	5(5)	2(2)		
Ebenaceae ^T	15(19)	3(7)	1(1)		
Elaeocarpaceae ^T	2(5)	1(2)	1(1)		
Fagaceae ^T	0(4)	0(1)			1(1)
Flacourtiaceae	12(13)	4(8)			1(1)
Hamamelidaceae ^T	1(1)	1(1)	0(1)		
Hernandiaceae	1(1)				
Juglandaceae ^T		1(1)			
Lacistemataceae		1(1)			
Lamiaceae ^T		1(1)			
Lecythidaceae	18(21)	1(1)			
Leeaceae	1(1)				
Loganiaceae	1(1)	1(2)			1(1)
Lythraceae ^T	2(2)	2(3)	0(2)	1(1)	
Malvaceae ^T	1(3)	2(4)	0(1)	1(1)	
Meliaceae	28(41)	16(25)	4(4)		1(1)
Meliantaceae		0(1)		1(1)	
Moringaceae		1(1)			
Myrtaceae ^T	10(26)	23(12)			2(2)
Oleaceae ^T	2(2)				
Oxalidaceae ^T	1(1)				
Passifloraceae ^T	2(2)				
Phytolaccaceae ^T	3(3)				
Pinaceae ^T		1(1)		1(1)	
Polygalaceae ^T	9(9)				
Polygonaceae ^T		1(1)			
Proteaceae	1(1)	1(2)		1(1)	
Rhamnaceae ^T	2(6)	3(3)	0(3)		
Rutaceae ^T	5(7)	6(17)	0(1)	1(1)	
Salicaceae		1(1)			
Samydaceae	2(2)				
Sapindaceae ^T	29(35)	5(8)	2(2)	1(1)	
Sapotaceae ^T	12(37)	12(22)			2(2)
Solanaceae ^T	0(1)	1(1)			
Sonneratiaceae		2(2)			
Sterculiaceae	21(26)	16(21)	1(1)		
Thymeliaceae ^T	8(9)		1(1)		
Tiliaceae ^T	2(8)	8(15)		1(1)	
Urticaceae ^T		1(1)			
Violaceae ^T	2(2)				

^T Family is known to be represented by species with dormant seeds in temperate regions of the world (Baskin & Baskin 1998).

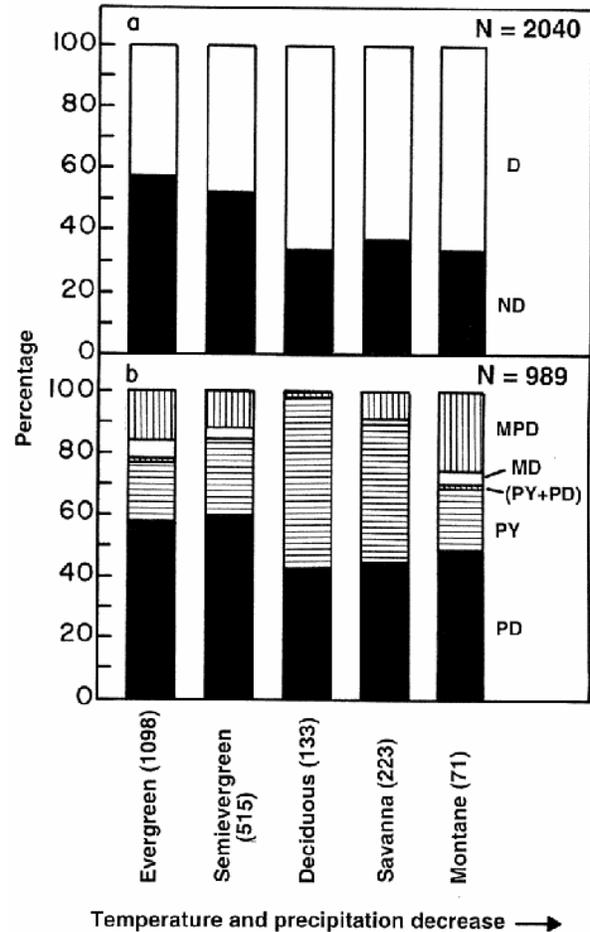


Fig. 1. Seed dormancy vs. nondormancy in 2040 species of climax tropical forest trees (a) and class of dormancy in 989 species of climax tropical trees (b) across the gradient of tropical forest types. Number of species in each forest type for which germination data are available is given in parenthesis. (a) Proportion of species with dormant and of those with nondormant seeds in each forest type (based on total number of species for each forest type). D = dormant, ND = nondormant. (b) Proportion of species with each class of seed dormancy in each forest type (based on total number of species with dormant seeds in each forest type). MPD = morphophysiological dormancy, MD = morphological dormancy, (PY + PD) = combination of physical dormancy and physiological dormancy, PY = physical dormancy, and PD = physiological dormancy.

Class of dormancy

Considering only the species with dormant seeds, the proportion of seeds with physiological dormancy was 43% or higher in all five forest types (Fig. 1b). Physiological dormancy decreased from evergreen to deciduous forests but increased slightly in savanna and montane forests, while physical dormancy increased from evergreen to savanna forests but decreased in the montane. Although morphophysiological dormancy decreased from evergreen to deciduous forests, it increased in savanna and montane forests. The increase in morphophysiological dormancy in the montane forests was accompanied by a decrease in physical dormancy, but physiological dormancy in the montane remained about comparable to that in the deciduous and savanna forests. Morphological dormancy was not very important in any of the five forest types, but it decreased from evergreen to savanna forests and then increased in montane forests.

Morphological dormancy (without any physiological dormancy) occurred in 28 species in seven families (Annonaceae, Araliaceae, Arecaceae, Magnoliaceae, Myristicaceae, Olacaceae, and Podocarpaceae) in the evergreen forests and in eight species in seven families (Annonaceae, Araliaceae, Icacinaceae, Myristicaceae, Olacaceae, Podocarpaceae, and Winteraceae) in the semievergreen forests. Morphological dormancy was not recorded for deciduous forests, and it occurred in two species of two families (Aquifoliaceae and Dilleniaceae) in savanna forests and in two species of two families (Canellaceae and Pittosporaceae) in montane forests.

Morphophysiological dormancy was recorded in 80 species in eight families (Annonaceae, Araliaceae, Arecaceae, Magnoliaceae, Myristicaceae, Olacaceae, Pittosporaceae, and Podocarpaceae) in evergreen forests, and it was found in 28 species in 10 families (Annonaceae, Aquifoliaceae, Araliaceae, Arecaceae, Canellaceae, Dilleniaceae, Icacinaceae, Magnoliaceae, Myristicaceae, and Olacaceae) in semievergreen forests. Morphophysiological dormancy occurred in one species of Arecaceae in deciduous forests and in 10 species in seven families (Annonaceae, Araliaceae, Arecaceae, Icacinaceae, Myristicaceae,

Opiliaceae, and Pittosporaceae) in savanna forests. In montane forests, morphophysiological dormancy was recorded in 12 species in seven families (Annonaceae, Aquifoliaceae, Araliaceae, Arecaceae, Monimiaceae, Myristicaceae, and Podocarpaceae).

Physical dormancy occurred in 88 species in eight families (Bixaceae, Bombacaceae, Fabaceae, Malvaceae, Rhamnaceae, Sapindaceae, Sterculiaceae, and Tiliaceae) in evergreen forests and in 62 species in six families (Bombacaceae, Fabaceae, Malvaceae, Sapindaceae, Sterculiaceae, and Tiliaceae) in semievergreen forests. Physical dormancy was present in 49 species in three families (Bombacaceae, Fabaceae, and Malvaceae) in deciduous forests, 64 species in two families (Bombacaceae and Fabaceae) in savannas, and 10 species in three families (Fabaceae, Sapindaceae, and Sterculiaceae) in the montane.

Physiological dormancy occurred in 282 species in 57 families in evergreen forest, 147 species in 47 families in semievergreen forests, 37 species in 15 families in deciduous forests, 63 species in 35 families in savannas, and 32 species in 15 families in montane forests. The combination of physical and physiological dormancy was recorded in one member of the Rhamnaceae in evergreen rainforests and in one member of this family in the montane forests.

Dormancy at the family level across the environmental gradient

All families represented by five or more species in one or more forest types are listed in Table 3. For each of these families, the number of species is given for each forest type, and the percentage with dormant seeds has been calculated. Table 3 allows us to examine the overall trend in change of proportion of species with dormant seeds for each family across the environmental gradient. In 19 of the 42 families, dormancy increased as temperature and precipitation decreased. However, in eight families there was no change, and in 12 families there was a decrease in proportion of species with dormancy as temperature and precipitation decreased. For three of the families, data are available only for the evergreen rain forest, so no comparison was possible.

Table 3. Families in which germination information is available for five or more species of climax trees in one or more tropical vegetation zones, number of species in each vegetation zone for which germination information is available (outside parentheses), percentage of species with dormant seeds (inside parentheses), and general overall trend in percentage of dormancy across the gradient of vegetation zones.

Family	Number of species (% with dormancy)					General trend in % of dormancy
	Evergreen	Semi- evergreen	Deciduous	Savanna	Montane	
Anacardiaceae	25(40)	13(23)	7(43)	4(50)	1(100)	+
Annonaceae ^b	35(100)	11(100)	x ^c	4(100)	1(100)	0
Apocynaceae	32(25)	10(30)	1(0)	6(17)	x	-
Araliaceae ^b	6(100)	3(100)	x	1(100)	1(100)	0
Areaceae ^b	27(100)	6(100)	1(100)	1(100)	2(100)	0
Bignoniaceae	17(6)	18(0)	1(0)	5(0)	1(0)	-
Bombacaceae	19(16)	11(27)	4(0)	8(13)	x	-?
Boraginaceae	3(100)	8(25)	6(100)	1(100)	2(50)	-?
Burseraceae	25(44)	4(75)	1(100)	x	x	+
Chrysobalanaceae	x	3(33)	x	5(60)	x	+
Clusiaceae	24(58)	12(50)	x	5(60)	x	0
Combretaceae	12(83)	9(11)	8(88)	5(60)	x	-
Dipterocarpaceae	71(2)	5(0)	2(0)	x	x	0
Ebenaceae	19(21)	7(57)	1(0)	3(100)	x	+
Elaeocarpaceae	5(60)	2(50)	1(0)	x	x	-
Euphorbiaceae	70(33)	20(45)	5(80)	5(40)	1(100)	+
Fabaceae	197(32)	81(52)	62(76)	93(68)	11(64)	+
Flacourtiaceae	13(8)	8(50)	x	3(33)	1(0)	+?
Irvingiaceae	6(100)	x	x	x	x	N
Lauraceae	30(73)	13(85)	x	3(100)	2(100)	+
Lecythidaceae	21(62)	1(0)	x	x	x	-
Melastomataceae	6(33)	3(33)	x	x	x	0
Meliaceae	41(32)	25(36)	1(100)	1(100)	1(0)	+
Moraceae	30(23)	18(17)	4(25)	3(33)	1(100)	+
Myrtaceae	26(62)	23(48)	x	6(50)	2(0)	-
Myristicaceae ^b	19(100)	4(100)	x	1(100)	1(100)	0
Olacaceae ^b	9(100)	2(100)	x	x	x	0
Polygalaceae	9(0)	x	x	x	x	N
Rhamnaceae	6(67)	3(0)	3(100)	1(100)	2(50)	+
Rhizophoraceae	7(86)	x	x	x	x	N
Rosaceae	13(77)	2(100)	x	x	3(33)	-
Rubiaceae	32(25)	13(69)	5(80)	4(75)	x	+
Rutaceae	7(29)	17(65)	1(100)	x	2(100)	+
Sapindaceae	35(17)	8(38)	2(0)	1(0)	1(100)	+
Sapotaceae	37(68)	22(46)	x	4(50)	x	-
Simaroubaceae	5(20)	3(67)	2(50)	1(100)	x	+
Sterculiaceae	26(19)	21(24)	1(0)	x	2(50)	+
Theaceae	3(33)	6(50)	x	x	x	+?
Thymeliaceae	9(11)	x	1(0)	x	x	-?
Tiliaceae	8(75)	15(47)	x	1(0)	x	-
Verbenaceae	10(40)	6(83)	1(100)	2(100)	1(100)	+
Vochysiaceae	7(57)	7(100)	x	9(100)	x	+

^a + = increase in proportion of species with seed dormancy, - = decrease in proportion of species with seed dormancy, 0 = no change in proportion of species with seed dormancy, N = not enough data to indicate a trend; ^b Seeds have underdeveloped embryos, thus they have either morphological or morphophysiological dormancy; ^c x = no data are available.

For many families, the number of tree species (with or without dormancy) decreases greatly across the environmental gradient. There are two possible reasons for this. One, several of the families in Table 3 are represented by trees in the evergreen and semievergreen forests, but they are represented mostly (sometimes only) by shrubs or herbaceous species in other types of forests. Two, for some families the low numbers of tree species shown in Table 3 in some forests may represent lack of research and not low number of species of trees in a particular family in a given type of forest.

Regardless of the type of vegetation, germination data are available for more species (444) of Fabaceae than for any other family. The economic value of many members of the Fabaceae no doubt contributes to the great amount of research effort that has been expended on learning how to propagate members of this family. Thus, for the Fabaceae we probably have a large enough sample from each of the five tropical forest types to make a meaningful comparison with regard to the trend in percentage of dormancy across the environmental gradient. The percentage of species with dormant seeds (i.e. physical dormancy) increases from 32% in the evergreen forest to 52-76% in the other tropical forest types. Consequently, there is an increase in dormancy, but many species with nondormant seeds occur in all of the forest types. We are somewhat surprised that there are species with nondormant seeds in the relatively dry deciduous and savanna forests. In contrast, all members of the legume family appear to have dormant seeds in the temperate zone regardless of habitat and life form (Baskin & Baskin 1998).

Discussion

We are in great need of detailed studies on dormancy break in seeds of tropical trees. It is well known that seeds of some tropical trees require many weeks, even months, for germination to occur (Msanga 1998; Ng 1973, 1978, 1980). The assumption is that these seeds are dormant and that dormancy break is occurring during the long interval between sowing and germination.

We know little about the temperature and moisture conditions required for dormancy break to occur. It is well known that physical dormancy

can be broken by scarification of the seed (or fruit) coat (Albrecht 1993; Msanga 1998; Watkins 1960), but is it possible to decrease the time required for dormancy break in seeds with physiological or morphophysiological dormancy by manipulation of environmental factors? It seems reasonable that tropical tree seeds with physiological dormancy would have the nondeep level of physiological dormancy, which can be broken by relatively high temperatures, depending on the species (Baskin & Baskin 1998; Nikolaeva 1977).

Assuming that tropical tree seeds with physiological dormancy have nondeep physiological dormancy, do seeds exhibit changes in their temperature requirements for germination as dormancy break occurs, like many species in temperate regions (*sensu* Baskin & Baskin 1998; Vegis 1964)? Five patterns of changes (or lack thereof) in temperature requirements for germination have been identified in various species whose seeds have nondeep physiological dormancy, i.e. five types of nondeep physiological dormancy are known. Information on the occurrence of the types of nondeep physiological dormancy in tropical species is needed to help us determine the possible evolutionary origins and relationships of the types of nondeep physiological dormancy.

Much additional work needs to be done on tropical members of families known to have physical dormancy, including detailed studies of the structure and mechanism of opening of the water gaps in the seed coat in some families, i.e. Cucurbitaceae, Rhamnaceae, and Sapindaceae (Baskin *et al.* 2000). Also, for the most part, we do not know how physical dormancy is broken in the various kinds of tropical forests, and we know little about the combination of physical and physiological dormancy in seeds of tropical trees. It seems quite possible that imbibition studies might help identify a few additional families with impermeable seeds (or fruits)!

Our expanded data base for tropical trees supports previous conclusions that there is an overall increase in dormancy with decrease in temperature and precipitation across the gradient of tropical forest types (Fig. 1). A very interesting aspect of this trend is that there are species with dormant seeds in the evergreen forest, and there are species with nondormant seeds in semievergreen, deciduous, savanna, and montane

forests. Thus, seed dormancy is present in the evergreen rainforests, and it does not “suddenly appear” in the relatively dry forest types, such as the deciduous or savanna forests. Further, seed dormancy does not prevent species from persisting in the wet forests, and it is not a requirement for persistence in dry forest.

Although temperature and precipitation generally decrease across the gradient of tropical forest types, we wonder if temperature and precipitation are the causes *per se* of the increase in seed dormancy. If they are, why does the proportion of species with dormant seeds remain about the same (actually decreases slightly) between deciduous and savanna forests instead of increasing? Perhaps, this slight decrease in dormancy is an artifact of the size of the data base for trees in deciduous and savanna forest types, and with the addition of data for other species the trend might be reversed. A second possible reason for the distribution of dormancy across the gradient may be related to phylogenetics, *i.e.* the way families with seed dormancy are distributed across the gradient. A third possible reason why deciduous, savanna, and montane forests have about the same proportion of species with dormant seeds is that seasonal variation in precipitation, and to some extent in temperature in the upper montane, results in the annual occurrence of a favorable and an unfavorable season for germination and subsequently for seedling establishment. It seems reasonable that an annual favorable and an unfavorable season for seedling establishment and survival might select for the evolution of seed dormancy. Consequently, one might expect to find more species with dormant seeds in seasonably variable habitats than in nonvariable ones. However, timing of seed maturation and dispersal might result in nondormant seeds falling on to the soil at the beginning of the wet (or warm) favorable season; thus, seed dormancy is not necessarily a requirement for persistence of a species in a seasonably variable habitat.

If we accept that seasonal variation plays a role in at least maintaining the presence of seed dormancy, why do some species in evergreen forests, where the environment supposedly is nonseasonal, have dormant seeds? Are the species with dormant seeds in the evergreen forests derived from ancestors that once grew in variable

environments, and is dormancy a “left-over” trait? Or, does the evergreen forest environment have favorable and nonfavorable times (“seasons”) for seed germination and seedling establishment that we have not been able to detect? Detailed information on the world biogeography of seed dormancy (or lack thereof) in families known to have species with dormant seeds in evergreen forests would provide valuable insight into origins of dormancy in these families, and especially in those in the wet evergreen forest habitat.

Depending on the family, dormancy increased, decreased, or did not change across the gradient of tropical forest types (Table 2). However, in a number of cases, a family was represented in a forest type by only one species, and seeds of that species were nondormant. Nine of 17 families with only nondormant seeds in evergreen rainforests were represented by only one species, 12 of 16 in semievergreen, 8 of 11 in deciduous, 8 of 10 in savanna, and 6 of 8 in montane. It seems likely that more research on members of these families (that presently are represented only by a single species with nondormant seeds) might result in the discovery of some species with dormant seeds. Thus, studies on additional members of under-represented families, especially in deciduous, savanna, and montane forests, would make a substantial contribution to understanding the germination ecology of tropical trees.

Many of the families listed in Table 2 for which no species had dormant seeds in one or more forest types have species in some other tropical forests types with dormant seeds. Further, a number of these families have species in the temperate region with dormant seeds (Baskin & Baskin 1998). Thus, studying members of the same family from a diversity of vegetation zones throughout the world would allow us to determine if the family has dormant (or nondormant) seeds in all the vegetation zones in which it occurs. Such information would contribute to a better understanding of the evolutionary and ecological aspects of seed dormancy in general and to tropical trees in particular.

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