

Classification and ecological relationships of seed dormancy in a seasonal moist tropical forest, Panama, Central America

Adriana Sautu^{1,2}, Jerry M. Baskin^{1*}, Carol C. Baskin^{1,3}, Jose Deago² and Richard Condit²

¹Department of Biology, University of Kentucky, Lexington, KY 40506-0225 USA; ²Smithsonian Tropical Research Institute, Panama City 34002-0948, Panama; ³Department of Plant and Soil Sciences, University of Kentucky, Lexington, KY 40546-0312 USA

Abstract

This is the first study to determine the class of seed dormancy (or non-dormancy) of a large number of native tree species in a tropical forest, the seasonal moist tropical forest of the Panama Canal Watershed (PCW), or to test the relationships between class of dormancy (or non-dormancy) and various seed and ecological characteristics of the constituent species. Fresh seeds of 49 of 94 tree species were non-dormant (ND), and 45 were dormant (D). Seeds of 23 species had physiological dormancy (PD), 13 physical dormancy (PY), two morphological dormancy (MD), 7 morphophysiological dormancy (MPD) and none combinational dormancy (PY + PD). Seeds with PY were significantly smaller (<0.1 g) and drier (moisture content < 16%) at maturity than those that were ND or in the other D classes. Seeds of 62, 42 and 53% of species dispersed in the early rainy, late rainy (LRS) and dry seasons, respectively, were ND. The majority (61%) of species with PD seeds, but only 17% of those with PY seeds, were dispersed in the LRS. The proportion of species with ND seeds was higher in large-size (63%) than in mid-size (35%) and understorey (17%) trees, but differed only slightly between non-pioneers (58%) and pioneers (54%). The proportion of species with D seeds increased only slightly through a precipitation gradient of about 3100 to 1900 mm in the PCW; however, PY increased from 19 to 32% and PD decreased from 63 to 44%.

Keywords: Panama Canal Watershed, precipitation gradient, seasonal moist tropical forest, seed dormancy classes, seed ecology

Introduction

Considerable diversity in the kinds of seed dormancy exists among plants (Nikolaeva, 1977; Nikolaeva *et al.*, 1985; Baskin and Baskin, 1998; 2004). Yet, most publications on seed dormancy have not indicated, or even suggested, the kind of dormancy that is investigated (Baskin and Baskin, 2004), and certainly there are no such studies at the community or vegetation-type level. Baskin and Baskin (2004) proposed a hierarchical classification system for seed dormancy, based on Nikolaeva (1977), that attempts to accommodate the diversity of the kinds of dormancy among seeds worldwide. The proposed system includes five classes (physiological, morphological, morphophysiological, physical and combinational) of dormancy and, within some of the classes, levels and types, i.e. levels within classes and types within levels.

Baskin and Baskin (2005) determined the proportion of tree species with non-dormant seeds, and of those within each of the five classes of dormancy, in the evergreen to deciduous tropical forest gradient on a worldwide scale from a list of >2000 species compiled from the literature. However, heretofore, no one has determined how non-dormancy and each of the five classes of dormancy are proportioned among species in a given (contiguous) area of tropical forest of any type. Neither has anyone investigated the relationship between the kind of seed dormancy (or non-dormancy) and the various seed or ecological characteristics of the constituent species at the community/vegetation-type level.

There are clear patterns of floristic spatial organization and of deciduousness, and other leaf traits, of species along the 1200 mm steep rainfall gradient of the 60 km of continuous seasonal moist tropical forest in the Panama Canal Watershed (PCW) (Pyke *et al.*, 2001; Condit *et al.*, 2004; Santiago *et al.*, 2004). The gradient across the PCW presents an excellent opportunity, not only to determine how seed non-dormancy and the five classes of seed dormancy

*Correspondence

Fax: +1 859 257 1717

Email: jmbask0@uky.edu

are distributed among species within a tropical forest, but also to test the relationship between the kinds of dormancy and climatic wetness/dryness within this forest. The purposes of this study were to: (1) classify (*sensu* Baskin and Baskin, 2004) the kinds of dormancy (and of non-dormancy) in seeds of the seasonal moist tropical forest of the PCW; (2) test the relationship between class of dormancy and seed mass, seed moisture content, dispersal season, tree colonizing status and tree growth form; and (3) test the relationship between the kind of dormancy and mean annual precipitation along the rainfall gradient.

Materials and methods

Site description

The PCW encompasses 2892 km² of land at 9° north latitude in the seasonal tropics. The mean annual temperature is 27°C. Mean annual rainfall varies from about 1600 mm yr⁻¹ on the Pacific coast to >3000 mm on the Caribbean coast. The dry season lasts 3–4 months from mid-December to mid-April (Condit, 1998). In this study, we divided the year into three precipitation seasons: dry (January–March), early rainy (April–July) and late rainy (August–December). The justification for doing this is discussed in Sautu *et al.* (2006). Most of the watershed is <300 m above sea-level, but elevation rises to 1000 m on three peaks to the south-west and east (Condit *et al.*, 2001).

In spite of the considerable variation in amount of rainfall and length of the dry season, mean annual precipitation is high enough to sustain a tall forest throughout the region. The general structure of forests of the canal area is quite similar, except for small areas of mangrove, freshwater swamps and mountain peaks. A closed canopy, 20–40 m tall with emergent trees reaching 50 m in height, and a dense understorey of saplings, treelets, palms and lianas can be found in well-drained sites (Condit *et al.*, 2001). The majority of the watershed (90%) is classified as tropical moist forest in the Holdridge (1967) system (Tosi, 1971). Large disturbances, such as hurricanes and fires, are absent; thus, individual treefalls and small windstorms are the sole natural source of canopy turnover. Sautu *et al.* (2006) contains a more detailed summary-description of the PCW.

Assignment to seed dormancy class

First, we grouped species into two categories: those with non-dormant seeds and those with dormant seeds. A seed was considered to be dormant if it had an underdeveloped embryo [i.e. one that must grow inside the seed before the radicle can emerge

(*sensu* Grushvitsky, 1967)], regardless of median length of germination time (MLG), or if the seeds had a fully developed embryo and MLG >30 d without any pretreatment. Seeds were considered as non-dormant if the embryos were fully developed and MLG was ≤30 d. Then, following Baskin and Baskin (2004), we further grouped the species with dormant seeds into five classes: (1) physical dormancy (PY), species with a water impermeable seed (or fruit) coat (always with a fully developed, non-dormant embryo); (2) morphological dormancy (MD), species with an underdeveloped embryo and an MLG ≤30 d; (3) morphophysiological dormancy (MPD), those with an undeveloped embryo and an MLG >30 d; (4) physiological dormancy (PD), those that have a water-permeable seed (or fruit) coat, a fully developed embryo and an MLG >30 d; and (5) combinational dormancy (PY + PD), species with a water-impermeable seed (or fruit) coat and a physiologically dormant (always fully developed) embryo.

A seed was considered to have PY or (PY + PD) if it did not imbibe water without pretreatment, and/or if the species belongs to a family or to one of its taxonomic subdivisions (e.g. *Anacardiaceae*, *Rhus* complex) known to have a water-impermeable seed (or fruit) coat (Baskin *et al.*, 2000). Water uptake (imbibition) was compared in scarified seeds (dipped in boiling water or mechanically scarified with a file or knife) versus non-scarified seeds of six species (*Apeiba aspera*, *Colubrina glandulosa*, *Enterolobium cyclocarpum*, *E. schomburgkii*, *Luehea seemannii* and *Ormosia macrocalyx*) suspected to have PY (because of the families to which they belong), and for which enough seeds were available for testing. Imbibition studies were also conducted on five additional species (*Andira inermis*, *Amaioua corymbosa*, *Ficus insipida*, *Heisteria concinna* and *Trema macrantha*) to resolve conflicting literature reports of water impermeability versus water permeability of their seeds. The diaspores (dispersal units) were weighed and placed on moist filter paper at room temperature (c. 22°C). Then, at time 0, and at various intervals for 24–48 h, seeds were removed from the wet paper, blotted dry and reweighed. Percentage water uptake was calculated as the actual increase in fresh seed mass, based on seed mass at time 0:

$$\%W_s = [(W_i - W_0)/W_0] \times 100,$$

where % W_s = percentage increase in seed mass, W_i = mass after a given interval of time and W_0 = seed mass at time 0. A considerable increase in mass indicates that the seed has a water-permeable coat, whereas no increase in mass indicates that it has a water-impermeable coat.

The effect of scarification on germination was also tested on seeds of the six species listed above suspected to have PY, for which imbibition curves

were prepared, and for *Guazuma ulmifolia*, *Luehea speciosa* and *Sapindus saponaria* that also belong to families in which seeds of some species have PY. Germination and imbibition curves for scarified versus non-scarified seeds, MLG and information in the literature on seed germination and/or taxonomic relationships were used to determine if a species had a water-impermeable or a water-permeable seed (or fruit) coat. Seeds with a water-impermeable coat that had an MLG ≤ 30 d after they were scarified would have PY, whereas those with a water-impermeable coat that had an MLG > 30 d after they were scarified would have (PY + PD).

Whether seeds had an underdeveloped or a fully developed embryo was determined by microscopic examination of the internal morphology of the seeds (if available) or by inference based on taxonomy, i.e. type of embryo reported for the genus or family (Baskin and Baskin, unpublished database for numerous genera and species in more than 300 families). Seeds with an underdeveloped embryo and an MLG ≤ 30 d had MD, and those with an underdeveloped embryo and an MLG > 30 d had MPD.

Seed and ecological characteristics of study species

Methods and results of studies on seed mass, seed moisture content, various germination parameters and the relationships between these measures for 100 tree species are reported in Sautu *et al.* (2006). Assignment of trees to growth form follows Hubbell and Foster (1986) and Condit *et al.* (1996a): large trees (≥ 20 m tall), mid-size trees (10–20 m) and understorey trees (4–10 m) (see Table 1). A species was assigned to the gap specialist or generalist category using the colonizing index of Condit *et al.* (1996b), which is based on a strong tendency to recruit in gaps (gap specialist) versus recruitment under forest canopy as well as in gaps (generalist).

Seed dormancy along the rainfall gradient

The Center for Tropical Forest Science (CTFS) has established a series of 1-ha inventory plots along the nearly continuous corridor of tall, closed-canopy forest that flanks the Panama Canal. The main purpose of these plots is for floristic and forest dynamic studies. We compared the proportion of species with each class of dormancy (including those with ND) along the gradient, based on inventory data from the CTFS for 39 of these permanent plots. Average annual rainfall in the plots ranges from 1887 to 3072 mm (Pyke *et al.*, 2001). We divided the entire range into five zones of equal-range units of mean annual precipitation: zone 1, 1887–2124 mm; zone 2,

2125–2360 mm; zone 3, 2361–2598 mm; zone 4, 2599–2835 mm; and zone 5, 2836–3072 mm. The number of our study species in the plots for each of the five zones was 53, 63, 76, 57 and 63, respectively. Then, the proportion of species with seeds in each class of dormancy (including ND) was calculated for each rainfall zone along the gradient.

Nomenclature follows D'Arcy (1987), except as updated by Condit *et al.* (1996a). Authors of scientific names are given in Sautu *et al.* (2006).

Results

Assignment to seed dormancy class

Based on various criteria, 49 (52.1%) species were non-dormant, and 45 (47.9%) were dormant (Table 1). Although we have no data to calculate MLG for *Beilschmiedia pendula*, its seeds were considered to be non-dormant since the germination period ended in less than 30 days. Seeds of *Cordia alliodora* were considered to be non-dormant based on a report in the literature (Salazar, 2000). Twenty-three (24.5%) of the species had PD, seven (7.4%) MPD, two (2.1%) MD and 13 (13.8%) PY (Table 1). No seeds had (PY + PD).

Species with non-dormancy and with physiological dormancy

Based on MLG, a fully developed embryo and a water-permeable seed or fruit coat, 72 species were assigned to ND or PD. Then, species with an MLG < 30 d were assigned to ND and those with an MLG > 30 d to PD, resulting in 49 species with ND and 23 with PD. Seeds of *Byrsonima crassifolia* and *Cordia alliodora* germinated to very low percentages (7 and 3.5, respectively). They were assigned to PD based on our germination data and on information in the literature (Vega *et al.*, 1983; Geilfus, 1994; Salazar, 2000; Correa, 2003).

Dipteryx oleifera, *Prioria copaifera* and *Tachigalia versicolor* (Fabaceae) belong to a family whose seeds are known to have fully developed embryos and PY, (PY + PD) and PD, or to be non-dormant (Baskin and Baskin, 1998, 2003). They were assigned to dormancy class PD based on an MLG > 30 d, and on their short longevity in storage in laboratory conditions at 20°C and 60% RH (Sautu *et al.*, 2006), which is inconsistent for seeds with impermeable seed coats (Tweddle *et al.*, 2003; Sautu *et al.*, 2006). According to Sandi and Flores (2002), seeds of *P. copaifera* are recalcitrant, and the seed coat is undifferentiated. Thus, the seeds certainly would not have PY. *Spondias mombin* and *S. radlkoferi* (Anacardiaceae) also belong to a family whose seeds are known to have fully developed embryos and PY,

Table 1. Class of seed dormancy for 94 species native to the Panama Canal Watershed and basis of assignment of each species to that class. ND, non-dormant; PD, physiological dormancy; PY, physical dormancy; MD, morphological dormancy; MPD, morphophysiological dormancy. MLG, median length of germination time in days. I, impermeable seed or fruit coat; P, permeable seed or fruit coat. FD, fully developed embryo; UD, underdeveloped embryo. Species growth form: T, large tree; M, medium-sized tree; U, understory tree. Species colonizing status: C, gap specialist; N, generalist

Family/species	Dormancy class	Basis of assignment
<i>Anacardiaceae</i>		
<i>Anacardium excelsum</i> (T)	ND	MLG ^a < 30 d, FD ^b , I/P ^c
<i>Spondias mombin</i> (T, C)	PD	MLG ^a > 30 d, FD ^b , I/P ^c
<i>Spondias radlkoferi</i> (T)	PD	MLG ^a > 30 d, FD ^b , I/P ^c
<i>Tapirira guianensis</i> (T)	ND	MLG ^a < 30 d, FD ^b , I/P ^c
<i>Annonaceae</i>		
<i>Annona spraguei</i> (M, C)	MPD	MLG ^a > 30 d, UD ^d , P ^e
<i>Xylopia aromatica</i> (M)	MPD	MLG ^a > 30 d, UD ^d , P ^e
<i>Xylopia frutescens</i> (M)	MPD	MLG ^a > 30 d, UD ^d , P ^e
<i>Apocynaceae</i>		
<i>Aspidopserma cruenta</i> (T, N)	ND	MLG ^a < 30 d, FD ^b , P ^e
<i>Lacmellea panamensis</i> (M)	ND	MLG ^a < 30 d, FD ^b , P ^e
<i>Araliaceae</i>		
<i>Dendropanax arboreus</i> (T)	MD	MLG ^a < 30 d, UD ^d , P ^e
<i>Schefflera morototoni</i> (T)	MD	MLG ^a < 30 d, UD ^d , P ^e
<i>Bignoniaceae</i>		
<i>Jacaranda copaia</i> (T, C)	ND	MLG ^a < 30 d, FD ^b , P ^e
<i>Tabebuia guayacan</i> (T)	ND	MLG ^a < 30 d, FD ^b , P ^e
<i>Tabebuia rosea</i> (T, N)	ND	MLG ^a < 30 d, FD ^b , P ^e
<i>Boraginaceae</i>		
<i>Cordia alliodora</i> (T, C)	ND	MLG ^a < 30 d, FD ^b , P ^e
<i>Burseraceae</i>		
<i>Bursera simaruba</i> (M)	ND	MLG ^a < 30 d, FD ^b , P ^e
<i>Protium panamense</i> (M, N)	ND	MLG ^a < 30 d, FD ^b , P ^e
<i>Protium tenuifolium</i> (M, N)	ND	MLG ^a < 30 d, FD ^b , P ^e
<i>Trattinnickia aspera</i> (T)	PD	MLG ^a > 30 d, FD ^b , P ^e
<i>Clusiaceae</i>		
<i>Calophyllum longifolium</i> (T, N)	ND	MLG ^a < 30 d, FD ^b , P ^e
<i>Euphorbiaceae</i>		
<i>Adelia triloba</i> (U, C)	ND	MLG ^a < 30 d, FD ^b , P ^e
<i>Hura crepitans</i> (T)	ND	MLG ^a < 30 d, FD ^b , P ^e
<i>Hyeronima alchoeroneoides</i> (T, C)	PD	MLG ^a > 30 d, FD ^b , P ^e
<i>Margaritaria nobilis</i> (U)	PD	MLG ^a > 30 d, FD ^b , P ^e
<i>Sapium glandulosum</i> (T)	PD	MLG ^a > 30 d, FD ^b , P ^e
<i>Fabaceae – Caesalpinioideae</i>		
<i>Cassia grandis</i> (T)	ND	MLG ^a < 30 d, FD ^b , I/P ^{f,g}
<i>Copaifera aromatica</i> (T)	ND	MLG ^a < 30 d, FD ^b , I/P ^{f,g}
<i>Dialium guianense</i> (T)	PY	MLG ^a > 30 d, FD ^b , I/P ^{f,g}
<i>Hymenaea courbaril</i> (T)	ND	MLG ^a < 30 d, FD ^b , I/P ^{f,g}
<i>Prioria copaifera</i> (T, N)	PD	MLG ^a > 30 d, FD ^b , I/P ^{f,g}
<i>Tachigalia versicolor</i> (T, N)	PD	MLG ^a > 30 d, FD ^b , I/P ^{f,g}
<i>Fabaceae – Faboideae</i>		
<i>Andira inermis</i> (T, N)	PD	MLG ^a > 30 d, FD ^b , I/P ^{f,g}
<i>Dalbergia retusa</i> (M)	ND	MLG ^a < 30 d, FD ^b , I/P ^f
<i>Diphysa robinoides</i> (M)	ND	MLG ^a < 30 d, FD ^b , I/P ^f
<i>Dipteryx oleifera</i> (T)	PD	MLG ^a > 30 d, FD ^b , I/P ^{f,g}
<i>Erythrina fusca</i> (T)	ND	MLG ^a < 30 d, FD ^b , I/P ^f
<i>Lonchocarpus latifolia</i> (T, C)	ND	MLG ^a < 30 d, FD ^b , I/P ^f
<i>Ormosia macrocalyx</i> (T)	PY	MLG ^a > 30 d, FD ^b , I/P ^{f,h,i}
<i>Pterocarpus rohrii</i> (T, N)	ND	MLG ^a < 30 d, FD ^b , I/P ^f

Table 1. Continued

Family/species	Dormancy class	Basis of assignment
<i>Fabaceae – Mimosoideae</i>		
<i>Albizia adinocephala</i> (T)	ND	MLG ^a < 30 d, FD ^b , I/P ^{f,g}
<i>Enterolobium cyclocarpum</i> (T)	PY	MLG ^a > 30 d, FD ^b , I/P ^{f,h,i}
<i>Enterolobium schomburgkii</i> (T)	PY	MLG ^a > 30 d, FD ^b , I/P ^{f,h,i}
<i>Inga punctata</i> (T)	ND	MLG ^a < 30 d, FD ^b , I/P ^{f,j}
<i>Inga spectabilis</i> (T)	ND	MLG ^a < 30 d, FD ^b , I/P ^{f,j}
<i>Pseudosamanea guachapele</i> (T)	PY	MLG ^a > 30 d, FD ^b , I/P ^{f,g}
<i>Flacourtiaceae</i>		
<i>Hasseltia floribunda</i> (M, N)	ND	MLG ^a < 30 d, FD ^b , P ^e
<i>Lindackeria laurina</i> (M)	PD	MLG ^a > 30 d, FD ^b , P ^e
<i>Humeriaceae</i>		
<i>Vantanea deplete</i> (T)	PD	MLG ^a > 30 d, FD ^b , P ^e
<i>Lauraceae</i>		
<i>Beilschmiedia pendula</i> (T, N)	ND	MLG ^a < 30 d, FD ^b , P ^e
<i>Phoebe cinnamomifolia</i> (T, C)	ND	MLG ^a < 30 d, FD ^b , P ^e
<i>Lecythydaceae</i>		
<i>Gustavia superba</i> (M, C)	PD	MLG ^a > 30 d, FD ^b , P ^e
<i>Lythraceae</i>		
<i>Lafoensia puniceifolia</i> (T)	ND	MLG ^a < 30 d, FD ^b , P ^e
<i>Malpighiaceae</i>		
<i>Byrsonima crassifolia</i> (U)	PD	MLG ^a > 30 d, FD ^b , P ^e
<i>Malvaceae s. lat.</i> (i.e. including <i>Bombaceae</i> , <i>Sterculiaceae</i> and <i>Tiliaceae</i>)		
<i>Apeiba aspera</i> (T)	PY	MLG ^a > 30 d, FD ^b , I/P ^{f,h,i}
<i>Apeiba tibourbou</i> (M)	PY	MLG ^a > 30 d, FD ^b , I/P ^{f,g,k}
<i>Cieba pentandra</i> (T)	D	MLG ^a < 30 d, FD ^b , I/P ^f
<i>Guazuma ulmifolia</i> (T)	PY	MLG ^a > 30 d, FD ^b , I/P ^{f,i}
<i>Hampea appendiculata</i> (M)	ND	MLG ^a < 30 d, FD ^b , I/P ^f
<i>Luehea seemannii</i> (T, C)	PY	MLG ^a > 30 d, FD ^b , I/P ^{f,g,i}
<i>Luehea speciosa</i> (M)	PY	MLG ^a > 30 d, FD ^b , I/P ^{f,g,i}
<i>Ochroma pyramidale</i> (M)	PY	MLG ^a > 30 d, FD ^b , I/P ^{f,g}
<i>Pachira quinata</i> (T)	ND	MLG ^a < 30 d, FD ^b , I/P ^f
<i>Pseudobombax septenatum</i> (T)	ND	MLG ^a < 30 d, FD ^b , I/P ^f
<i>Quararibea astrolepis</i> (T, N)	ND	MLG ^a < 30 d, FD ^b , I/P ^f
<i>Sterculia apetala</i> (T)	ND	MLG ^a < 30 d, FD ^b , I/P ^{f,g}
<i>Trichospermum galeottii</i> (M)	PY	MLG ^a > 30 d, FD ^b , I/P ^{f,g}
<i>Melastomataceae</i>		
<i>Miconia argentea</i> (M, C)	ND	MLG ^a < 30 d, FD ^b , P ^e
<i>Miconia minutiflora</i> (M)	PD	MLG ^a > 30 d, FD ^b , P ^e
<i>Meliaceae</i>		
<i>Carapa guianensis</i> (T)	ND	MLG ^a < 30 d, FD ^b , P ^e
<i>Cedrela odorata</i> (T)	ND	MLG ^a < 30 d, FD ^b , P ^e
<i>Guarea guidonia</i> (M, N)	PD	MLG ^a > 30 d, FD ^b , P ^e
<i>Swietenia macrophylla</i> (T)	ND	MLG ^a < 30 d, FD ^b , P ^e
<i>Trichilia hirta</i> (T)	ND	MLG ^a < 30 d, FD ^b , P ^e
<i>Trichilia tuberculata</i> (T, N)	ND	MLG ^a < 30 d, FD ^b , P ^e
<i>Moraceae</i>		
<i>Brosimum utile</i> (T)	ND	MLG ^a < 30 d, FD ^b , P ^e
<i>Castilla elastica</i> (T)	ND	MLG ^a < 30 d, FD ^b , P ^e
<i>Ficus insipida</i> (T)	ND	MLG ^a < 30 d, FD ^b , P ^{e,h}
<i>Myristicaceae</i>		
<i>Virola sebifera</i> (M, N)	MPD	MLG ^a > 30 d, UD ^d , P ^e
<i>Virola surinamensis</i> (T)	MD	MLG ^a < 30 d, UD ^d , P ^e
<i>Olacaceae</i>		
<i>Heisteria concinna</i> (M, N)	MPD	MLG ^a > 30 d, UD ^d , P ^e
<i>Rhamnaceae</i>		
<i>Colubrina glandulosa</i> (T)	PY	MLG ^a > 30 d, FD ^b , I ^{h,i}
<i>Rubiaceae</i>		
<i>Alseis blackiana</i> (T, N)	ND	MLG ^a < 30 d, FD ^b , P ^e
<i>Amaioua corymbosa</i> (U)	MPD	MLG ^a > 30 d, UD ^d , P ^e

Table 1. *Continued*

Family/species	Dormancy class	Basis of assignment
<i>Antirhea trichantha</i> (M)	PD	MLG ^a > 30 d, FD ^d , P ^e
<i>Calycophyllum candidissimum</i> (T)	ND	MLG ^a < 30 d, FD ^b , P ^e
<i>Faramea occidentalis</i> (U, N)	PD	MLG ^a > 30 d, FD ^b , P ^e
<i>Genipa americana</i> (T)	ND	MLG ^a < 30 d, FD ^b , P ^e
<i>Guettarda foliacea</i> (U, N)	PD	MLG ^a > 30 d, FD ^b , P ^e
<i>Posoqueria latifolia</i> (M)	PD	MLG ^a > 30 d, FD ^b , P ^e
<i>Sapindaceae</i>		
<i>Cupania latifolia</i> (T)	PD	MLG ^a > 30 d, FD ^b , I/P ^{f,g}
<i>Sapindus saponaria</i> (M)	PD	MLG ^a > 30 d, FD ^b , I/P ^{f,g,i}
<i>Sapotaceae</i>		
<i>Chrysophyllum cainito</i> (T, C)	ND	MLG ^a < 30 d, FD ^b , P ^e
<i>Ulmaceae</i>		
<i>Trema macrantha</i> (M)	PD	MLG ^a > 30 d, FD ^b , P ^{e,h}
<i>Vochysiaceae</i>		
<i>Vochysia ferruginea</i> (T)	ND	MLG ^a < 30 d, FD ^b , P ^e

^aMLG, Sautu *et al.* (2006).

^bFD, family has fully developed embryos (Baskin *et al.*, 2000; unpublished database). See Sautu (2004) for drawings of embryos of *Apeiba aspera*, *Ficus insipida*, *Guarea guidonea*, *Luehea seemannii*, *Trema micrantha* and *Trichilia hirta*.

^cI/P, family has taxa with water-impermeable (I) and with water-permeable (P) endocarp; tribe *Spondidiae*, to which the three genera listed here belong, have a water-permeable endocarp (and seed coat) (Baskin and Baskin, 2000, unpublished database).

^dUD, family has underdeveloped embryos (Baskin and Baskin, 1998, unpublished database). See Sautu (2004) for photographs of underdeveloped embryos of *Amaioua corymbosa* and *Heisteria concinna*.

^eP, family has water-permeable seed coats only; not listed by Baskin *et al.* (2000) as a family with water-impermeable seed coat.

^fI/P, family has taxa with water-impermeable (I) and those with water-permeable (P) seed coats. Seed coats of species, with an MLG < 30 d in these families, were assumed to be water-permeable, i.e. seeds non-dormant.

^gSee text for additional information on assignment of seeds of this species to dormancy class.

^hScarification did not increase water uptake in seeds of *Andira inermis*, *Amaioua corymbosa*, *Ficus insipida*, *Heisteria concinna* or *Trema macrantha*, whereas it did increase water uptake in *Apeiba aspera*, *Colubrina glandulosa*, *Enterolobium cyclocarpum*, *E. schomburgkii*, *Luehea seemannii* and *Ormosia macrocalyx* (Sautu, 2004).

ⁱScarification increased germination in seeds of *Apeiba aspera*, *Colubrina glandulosa*, *Enterolobium cyclocarpum*, *E. schomburgkii*, *Guazuma ulmifolia*, *Luehea seemannii*, *L. speciosa*, *Ormosia macrocalyx* and *Sapindus saponaria* (Sautu, 2004).

^jSeeds of *Inga* spp. are non-dormant and recalcitrant (Pritchard *et al.*, 1995).

^kSeeds of *Apeiba tiburbou* are water impermeable (Daws *et al.*, 2006).

^lFamily generally with fully developed embryos (Baskin and Baskin, unpublished database), but *Amaioua corymbosa* has an underdeveloped embryo (Sautu, 2004).

(PY + PD) and PD, or to be non-dormant (Baskin and Baskin, 2003). However, seeds of these two species were assigned to dormancy class PD based on an MLG > 30 d, on after-ripening in dry storage (Sautu *et al.*, 2006) and on the high moisture content of fresh seeds, which is inconsistent with the presence of PY, and the fact that PY is not known to occur in tribe *Spondidiae*, to which they belong (Baskin *et al.*, 2000).

Species with morphological or morphophysiological dormancy

Seeds of *Dendropanax arboreus* (*Araliaceae*) were assigned to dormancy class MD, based on an MLG < 30 d and on the fact that members of the family *Araliaceae* have underdeveloped embryos (Baskin and Baskin, 1998, unpublished database). Seeds of *Virola*

surinamensis (Myristicaceae) were assigned to MD because they have an underdeveloped embryo (Piña-Rodrigues and Figliolia, 2005) and an MLG <30 d (Table 1).

Seeds of *Annona spraguei*, *Xylopia aromatica*, *X. frutescens* (Annonaceae), *Virola sebifera* (Myristicaceae) and *Schefflera morototoni* (Araliaceae) were assigned to dormancy class MPD, based on an MLG >30 d and on the fact that these families have underdeveloped embryos (Baskin and Baskin, 1998, unpublished database). *Heisteria concinna* (Olacaceae) and *Amaioua corymbosa* (Rubiaceae) had a water-permeable seed coat, an underdeveloped embryo (Sautu, 2004) and an MLG >30 d (Table 1); thus, they also were assigned to dormancy class MPD.

Species with physical dormancy

Scarified seeds of *Apeiba aspera*, *Colubrina glandulosa*, *Enterolobium cyclocarpum*, *E. schomburgkii*, *Luehea seemannii* and *Ormosia macrocalyx* imbibed water (% W_s >80), whereas few or no non-scarified seeds did so, demonstrating that these six species have water-impermeable seed coats. A small proportion of the intact seeds of *A. aspera* and *E. schomburgkii* were permeable (2 and 15%, respectively). However, there was no difference in water uptake of scarified versus non-scarified seeds of *Andira inermis*, *Amaioua corymbosa*, *Ficus insipida*, *Heisteria concinna* or *Trema macrantha*, demonstrating that they do not have PY.

Mechanical scarification, without further dormancy breaking treatment, increased germination significantly in fresh seeds of *Apeiba aspera*, *Colubrina glandulosa*, *Enterolobium cyclocarpum*, *E. schomburgkii*, *Guazuma ulmifolia*, *Luehea seemanni*, *L. speciosa*, *Ormosia macrocalyx* and *Sapindus saponaria*, suggesting that these species have PY only, i.e. not (PY + PD) (however, see comments in the Discussion regarding the assignment of seeds of *S. saponaria* to dormancy class PD and not to PY). The germination percentage of seeds of *Luehea speciosa* decreased from 22% (fresh seeds) to 4% after 5 months of dry storage, and 8-month-old seeds pretreated for 2 min with hot water germinated to 36% (versus 12% in control). These data suggest that seeds became dormant in storage, as reported for seeds of *L. divaricata* (Ramalho Carvalho, 1994). Germination percentages of seeds of *Apeiba tibourbou* and *Cassia grandis* did not vary significantly with pretreatment (Sautu, 2004).

Seeds of *Dialium guianense*, *Pseudosamanea guachapele* (Fabaceae), *Apeiba tibourbou* and *Luehea speciosa* (Tiliaceae s. str.) were assigned to dormancy class PY, based on data from our germination test results, information in the literature and/or characteristics of seeds in that family and/or genus (Baskin *et al.*, 2000). Seeds of *Apeiba tibourbou* germinated to a higher

percentage after treatment with sulphuric acid, and germination percentages of non-stored seeds of *Luehea seemannii* increased after immersion in hot water (Acuña and Garwood, 1987). Recently, Daws *et al.* (2006) reported that 80–100% germination was obtained in seeds of *A. tibourbou* by mechanically scarifying the seed coat or by removing the chalazal plug, either by mechanical scarification or hot-water treatment (100°C, 2 min). Based on literature reports that scarification caused a large increase in germination percentage, PY was assigned to seeds of *Ochroma pyramidale* (= *O. lagopus*, Bombacaceae s. str.) (Vázquez-Yañez, 1974; Vázquez-Yañez and Perez-García, 1976) and *Guazuma ulmifolia* (Sterculiaceae s. str.) (Acuña and Garwood, 1987). Seeds of these two species also had water-impermeable seed coats and an MLG >30 d (Table 1).

Characteristics of seeds with each kind of dormancy

All ecological data for the comparisons made in this section can be found in Table 1 of Sautu *et al.* (2006). Seed size and dormancy class were known for 90 species. The small number of species with MPD (7) and MD (2) are considered as one group for the purpose of comparison between classes of dormancy. Seeds of 8 of the 16 species (50%) with a mass of 1–10 g had PD, 7 had ND and 1 MPD. Seeds with PY are significantly smaller than those with ND, PD and MPD, which did not differ (Tukey HSD test, $P < 0.05$) (Fig. 1a). *Virola surinamensis* (2.9 g) is an extreme case in class MPD. Seeds with a mass >2.5 g are extremes or outliers in the ND category (*Anacardium excelsum*, *Aspidosperma cruenta*, *Brosimum utile*, *Calophyllum longifolium*, *Carapa guianensis*, *Hymenaea courbaril* and *Inga spectabilis*); seeds with a mass >3 g are outliers or extremes in the PD category (*Gustavia superba*, *Prioria copaifera*, *Spondias radlkoferi* and *Vantanea depleta*); and seeds with a mass >0.1 g are extremes in the PY category (*Dialium guianense*, *Enterolobium cyclocarpum* and *Ormosia macrocalyx*).

For 89 species to which dormancy class was assigned, we know the moisture content (MC) of fresh seeds. Seeds with PY have lower moisture contents than those in the other dormancy classes, which did not differ (Tukey HSD test, $P < 0.05$) (Fig. 1b).

Dispersal season and dormancy class were known for 94 species. Differences in class of dormancy between dispersal seasons are significant (chi-square = 0.05). Seeds of the majority of species with PD are dispersed in the late rainy season (60.9%), those with PY mainly in the dry and early rainy seasons (84.7%) and those that are non-dormant, year-round (Fig. 2a).

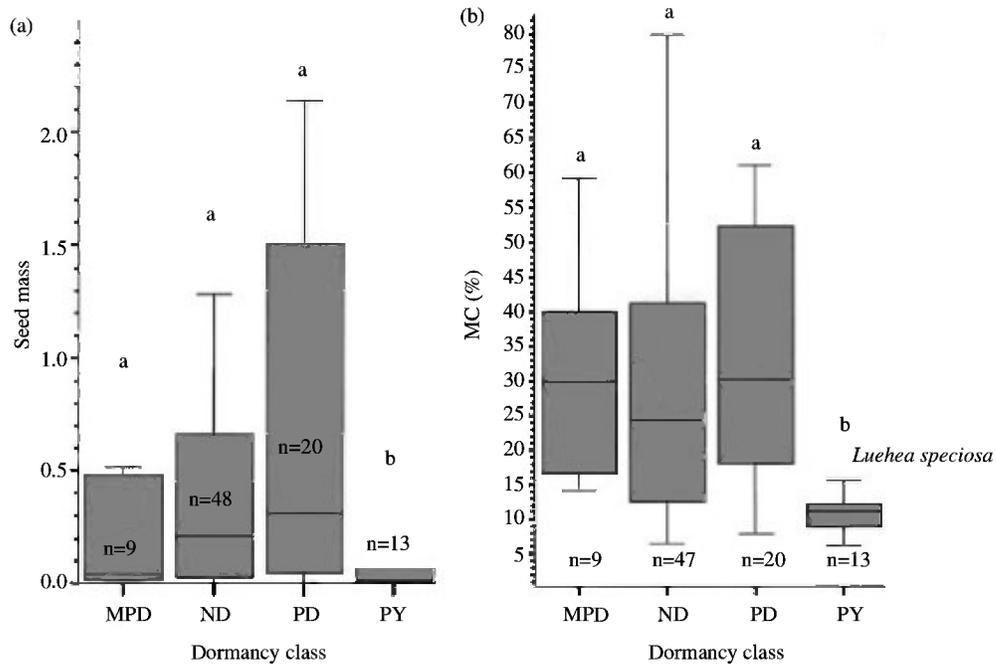


Figure 1. Seed mass (a) and moisture content (MC) (b) for non-dormant seeds and for each class of dormancy. MPD, morphological and morphophysiological dormancy (combined); ND, non-dormant; PD, physiological dormancy; PY, physical dormancy. For seed mass, letters represent subsets with significant differences (Tukey HSD test, $P < 0.05$). See text for information on outliers and extremes. For seed MC, the circle represents an outlier (*Luehea speciosa*), and letters represent subsets with significant differences (Tukey HSD test, $P < 0.05$).

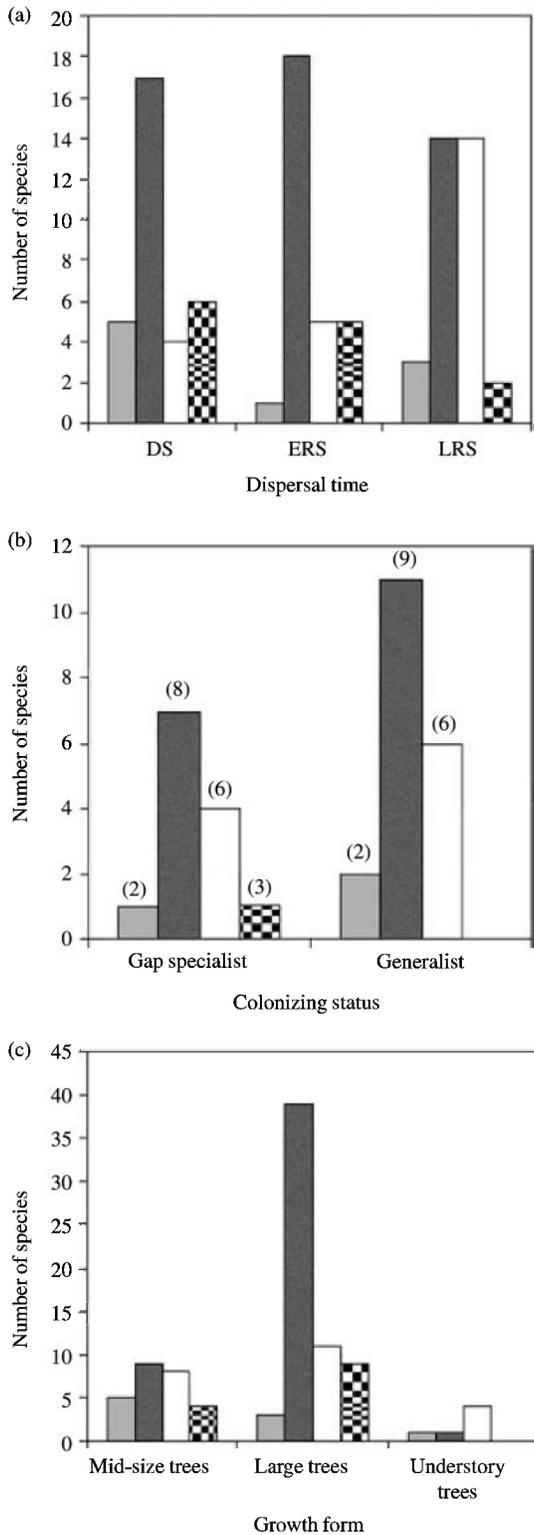
Colonizing status was known for 32 species. Differences in the distribution of dormancy classes between gap specialist and generalist species are not significant (chi-square > 0.05) (Fig. 2b). In his phytosociological analysis of the forest on Barro Colorado Island (BCI), Knight (1975) established the categories of 'infrequent reproducers', i.e. secondary species not reproducing in forest understorey, and 'frequent reproducers', i.e. climax or near-climax species reproducing in the forest understorey. Nineteen of Knight's infrequent reproducers and 17 of his frequent reproducers are included in our study. The frequency distribution of dormancy classes in Knight's infrequent reproducers and frequent reproducers and in our gap specialists and generalists are quite similar (Fig. 2b). In all cases, seeds of most of the species are non-dormant (42.1–57.9%) or have PD (30.1–35.3%). Further, seeds with PY occur (albeit with low frequency) in gap specialists and in infrequent reproducers, but not in generalists or frequent reproducers.

Growth form was known for all 94 species for which class of dormancy (or non-dormancy) was determined (Table 1). Difference in class of dormancy between large trees (≥ 20 m in height), mid-size trees (10–20 m) and understorey trees (4–10 m) was

statistically significant (chi-square < 0.05) (Fig. 2c). The majority of large trees have ND seeds followed by those with PD, PY, MD and MPD. Thirty-five percent of the 26 species of mid-size trees have non-dormant seeds, 31% PD, 19% MPD and 15% PY. Seeds of one of the six understorey trees are ND, and four have PD, one MPD and none PY or MD.

Dormancy and non-dormancy along the rainfall gradient

Ninety-two species whose dormancy class was established in this study were present in the set of 39 inventory plots that flank the Panama Canal. The first region (1887–2124 mm of precipitation annually) had a total of 53 species present; the second (2125–2360 mm), 63; the third (2361–2598 mm), 76; the fourth (2599–2835 mm), 57; and the fifth (2836–3072 mm), 63. The proportion of species with ND and PD decreased with decrease in rainfall, that with PY and MPD increased and that with MD was always very low; PY was the only dormancy class with a significant correlation coefficient ($P < 0.05$) (Fig. 3).



Discussion

In her study of seed germination of tree species on BCI in the centre of the PCW, Garwood (1983) defined length of dormancy (MLD) as number of days from sowing to germination. Based on an MLD of 4 weeks, about 50% of 157 species that germinated in her study were dormant (Garwood, 1983). Based on the median length of dormancy (MLG) and 30 d as the time-line between dormancy and non-dormancy, the proportion of tree species with dormant seeds for the whole PCW (48% of 94 species) in our study was nearly the same as that reported by Garwood (1983) for BCI. Furthermore, the proportion of seeds that were ND and of those in the different classes of dormancy for the whole PCW (ND = 52%, MD = 2%, MPD = 7%, PD = 25% and PY = 14%) differ only a little from proportions reported for tropical semi-evergreen forests (= seasonal moist tropical forest in present study) for worldwide samples of 467 (Baskin and Baskin, 2003) and 515 (Baskin and Baskin, 2005) species of trees.

The 13 species with PY (Table 1) occur in only three of the 16 families in which this class of dormancy has been confirmed (Baskin *et al.*, 2000; Baskin *et al.*, 2006): *Fabaceae*, *Malvaceae s. lat.* (including *Bombacaceae s. str.*, *Sterculiaceae s. str.* and *Tiliaceae s. str.*, *sensu* Angiosperm Phylogeny Group, 2003) and *Rhamnaceae*. Seeds of the four species of *Anacardiaceae* and *Sapindaceae*, the only other families included in our study that contain taxa whose seeds have PY, were either ND or had PD. Of the 20 species of *Fabaceae*, 11 were ND, 4 had PD and 5, PY. In contrast, seeds produced by members of this family in temperate and arctic regions almost always have PY, but a few have (PY + PD) (Baskin and Baskin, 1998).

Several of the species listed in Table 1 that belong to families containing both taxa with water-impermeable and water-permeable seed coats require additional comments about assignment to seed dormancy class. Based on a germination percentage of 52% and an MLG < 30 d, we assigned seeds of *Hymenaea courbaril* (*Fabaceae*) to the non-dormant



Figure 2. Distribution of species in each class of dormancy (including non-dormancy) in relation to (a) dispersal time, (b) colonizing status and (c) growth form. DS, dry season (January–March); ERS, early rainy season (April–July); LRS, late rainy season (August–December). MPD, morphophysiological and morphological dormancy (combined); ND, non-dormancy; PD, physiological dormancy; PY, physical dormancy. Numbers in parenthesis above bars for gap specialists and generalists indicate number of species of Knight's (1975) 'infrequent reproducers' and 'frequent reproducers', respectively, included in our study. ■ ND, □ PD, ■ MPD + MD, ▨ PY.

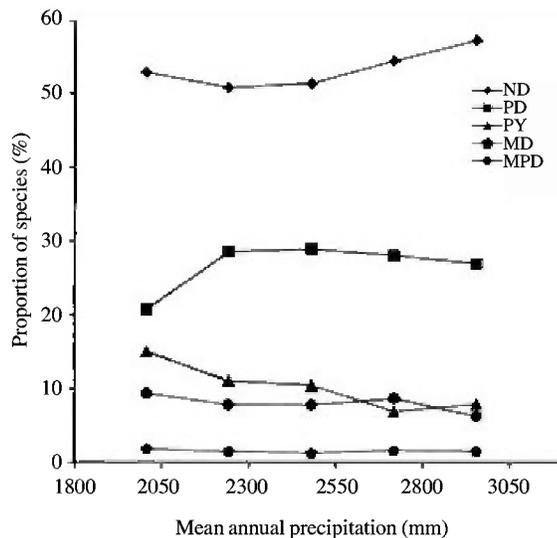


Figure 3. Distribution of the proportion of species with seeds in each dormancy class (including non-dormancy) through the rainfall gradient along the Panama Canal. Regions are defined by mean annual precipitation. Seed dormancy class: ND, non-dormant; PD, physiological dormancy; PY, physical dormancy; MPD, morphophysiological dormancy; MD, morphological dormancy.

category. However, seeds of this species have been reported to have a water-impermeable seed coat, and thus PY (Brahmam, 1996; Almeida *et al.*, 1999). Seeds of *Cassia grandis* (*Fabaceae*) in our study germinated to 43% and had an MLG <30 d. Thus, we concluded that they were non-dormant. However, Flores *et al.* (1986) reported that seeds of this species had a water-impermeable seed coat and initiated germination 45 d after they were sown (i.e. PY). Thus, it is likely that the seeds of these two species that did not germinate in our study had PY. Seeds of *Dialium guianense* (*Fabaceae*) had an MLG <30 d, but they germinated to only 2.8%. We assigned seeds of this species to PY, based on a report by Gill and Bamidele (1981) that the seed coat is water impermeable. Our assignment of seeds of *Copaifera aromatica* (*Fabaceae*) to the non-dormant category (73% germination, MLG <30 d) agrees with a report by Jimenez (1993, cited in Marin and Flores, 2002a) that seeds of this species collected in northern Costa Rica germinated to 85% after soaking for 24 h in running water, and with reports that seeds of the congeners *C. camibar* (Marin and Flores, 2002b) and *C. multijuga* (Ferraz *et al.*, 2004) are also non-dormant. In contrast to many other reports that seeds of *Albizia* spp. have PY (Baskin and Baskin, 1998), our results indicate that those of *Albizia adinocephala* (*Fabaceae*) are non-dormant (77% germination, MLG = 7 d) (Sautu *et al.*, 2006). Fresh seeds of *Pseudosamanea guachapele* (*Fabaceae*) have been reported to germinate to 60–70%

without pretreatment, to 82% after scarification with hot water (80°C) and to 90% after mechanical scarification (Flores, 2002). However, in our study, seeds germinated to only 13%, and MLG was 81 d. Thus, since this species belongs to the *Fabaceae*, we assigned the seeds to dormancy class PY. Perhaps, seeds that germinated to high percentages in the studies summarized by Flores (2002) had not dried to a moisture content low enough to make them water impermeable (see Baskin and Baskin, 1998).

Seeds of *Cupania latifolia* (*Sapindaceae*) germinated to 58%, and MLG was 73 d (Sautu *et al.*, 2006). Thus, we assigned them to PD. We know of no previous reports on the germination behaviour of this species, but Garwood (1983) reported that seeds of the congener *C. sylvatica* from BCI germinated to 100% and had an MLD of 3.0 d. Thus, the seeds were non-dormant. Intact seeds of *Sapindus saponaria* (*Sapindaceae*) in our study germinated to only 5.2% with an MLG of 74 d, and seeds mechanically scarified germinated to 64% in <30 d (Sautu, 2004). Various treatments have been reported to break seed dormancy in this genus, including scarification with concentrated sulphuric acid or hot water followed by cold stratification (Munson, 1984); soaking in concentrated sulphuric (Vora, 1989; Brahmam *et al.*, 1996; Naidu *et al.*, 1999), nitric and hydrochloric acids (Naidu *et al.*, 1999); soaking in a cow-dung slurry (Brahmam *et al.*, 1996); exposing seeds to temperatures in the range of 30–100°C for various periods of time (Naidu *et al.*, 1999); and treating seeds with the plant growth regulators gibberellic acid (GA₃), indole butyric acid (IBA) and indole acetic acid (IAA) (Naidu *et al.*, 2000). Since GA₃, IBA and IAA, and especially GA₃, overcame dormancy in nearly fresh intact seeds of *S. trifoliatum*, we assigned seeds of *S. saponaria* to dormancy class PD. Negi and Todaria (1993) even found that fresh seeds of *S. mukorossi* were non-dormant, germinating up to 99% without pretreatment.

In the Garwood (1983) study, *Sterculia apetala* (*Malvaceae s. lat.*) germinated to 55% and had an MLD of 31.8 d. In our study, seeds of *S. apetala* germinated to 37% with an MLG of 9 d (Sautu *et al.*, 2006). Thus, we assigned seeds of this species to the non-dormant category, as has been reported for several other species of this genus (Baskin and Baskin, 1998). Non-treated seeds of *Luehea speciosa* (*Malvaceae s. lat.*) germinated to 22% and had an MLG of 14.5 d in our study (Sautu *et al.*, 2006). Treatment with hot water increased germination of seeds dry-stored for 8 months from 12% (control) to 36% (Sautu, 2004). In the congener *L. seemannii*, Pearson *et al.* (2002) obtained c. 50% germination in non-treated seeds of this species at 30°C in both light and dark, and up to 70–80% over a range of diurnal fluctuating temperatures in light. In our study, scarification with hot water increased

germination from 38 to 62% (Sautu *et al.*, 2006). Acuña and Garwood (1987) also showed that hot-water scarification significantly increased germination in this species. Thus, based on significant increases in germination percentages by hot-water treatment, we assigned the two species of *Luehea* to the PY class of dormancy. In our study, seeds of *Trichospermum galeottii* (*Malvaceae* s. lat.; = *T. mexicanum*, see Condit *et al.*, 1996a) germinated to only 15% with an MLG of 31 d (Sautu *et al.*, 2006). For non-treated seeds of *T. galeottii*, Pearson *et al.* (2002) obtained <5% germination at 30°C in both light and dark. However, about 50% of hot-water scarified seeds planted a few millimetres below the soil surface germinated at 30/24°C. Acuña and Garwood (1987) also showed that both acid and hot-water scarification increased germination in seeds of this species. Thus, we conclude that seeds of *T. galeottii* have PY.

The distribution of length of seed dormancy is a continuum (Garwood, 1983), and thus the proportion of dormant and non-dormant seeds will vary depending on the arbitrary line drawn between dormancy and non-dormancy. *Carapa guianensis*, *Chrysophyllum cainito*, *Dipteryx oleifera*, *Hyeronima alcheoraeoides* and *Prioria copaifera* are examples of species whose seeds have been considered to be both dormant and non-dormant, i.e. in studies using seeds from different provenances and tested in different conditions. The small differences between the results of the present study and those by Baskin and Baskin (2003, 2005) may be due to the arbitrary limit between classifying seeds as dormant or non-dormant, as well as the lack of information on underdeveloped versus fully developed embryos and on water-impermeable versus water-permeable seed (or fruit) coats.

Garwood (1983) considered that germination time for species is controlled by dispersal time in the early rainy season, by seed dormancy in the late rainy season and equally by seed dormancy and timing of dispersal in the dry season. In agreement with this statement, our results show that the majority of species dispersed during the early rainy season are non-dormant (62%), and within dormancy classes PY and PD are equally represented (17% each). In the late rainy season, the majority of the species are dormant (58%), and PD is more common than other dormancy classes (PD 42%; MPD 9%; PY 6%). Also, in agreement with MLD reported by Garwood (1983), the delay of germination is longer than that in the dry and early rainy seasons (Sautu *et al.*, 2006). The number of species dispersed in the dry season with ND seeds almost equals that of species with dormant seeds (ND 53%; PY 19%; MPD 16% and PD 12%), and PY appears to be slightly favoured (40%) within dormancy classes.

The majority of species with PY seeds are dispersed in the dry (46%) and early rainy (39%) seasons. Only 2 of the 13 species (15%) with PY were dispersed in the late rainy season, and both of them have a long fruiting period that includes the dry season. *Pseudosamanea guachapele* begins fruiting in the late rainy season and continues to do so throughout the dry season, and *Ormosia macrocalyx* begins to fruit at the end of the dry season and continues to do so throughout the rainy season. The majority of species dispersed during the early rainy season are non-dormant (62%), and the dormancy classes represented are PY (17%), PD (17%) and MPD (4%). Following Garwood's (1983) interpretation, in the early rainy season the main mechanism controlling germination time is timing of dispersal. Seed dormancy is also present, and both PY and PD appear to be equally favoured. Nevertheless, from dry to rainy situations, PY appears to decrease and PD to increase.

Seeds of the majority of species (57%) with MPD are dispersed in the dry season, 29% in the late rainy season and 14% in the early rainy season. Morphologically dormant seeds represent a very small proportion of the total species, which is similar to what Baskin and Baskin (1998) reported. One of the two species with MD is dispersed in the early rainy season and one in the late rainy season.

The majority of large trees (63%) have non-dormant seeds, and the majority of mid-size trees have dormant seeds (65%). Our sample size for understorey trees (only six species) may not be representative. Nevertheless, the trend is for an increase in PD as tree height decreases, and PY is absent in the understorey. In agreement with these results, Baskin and Baskin (1998) reported that PD is more common in shrubs than in trees in tropical semi-evergreen forests and that PY is more important in trees than in shrubs. Sample size is inadequate for species whose seeds have MD, which are represented by only two species. More information is needed about kind of embryos (i.e. underdeveloped versus fully developed) in tropical tree seeds to determine the class of dormancy to which the seeds belong.

The pioneer/shade tolerant dichotomy (Swaine and Whitmore, 1988; Whitmore, 1989) is best described as a continuum (Alvarez-Buylla and Martínez-Ramos, 1992), and the majority of species native to the PCW fell in a narrow range of intermediate values for demographic variables (Condit *et al.*, 1996b). Moreover, pioneer species on Barro Colorado Island exhibit a variety of seed sizes, seed dormancy patterns, timing of reproduction and seed dispersal agents (Dalling *et al.*, 1997). The distribution of classes of dormancy for the 32 species

with a confident classification as gap specialists or generalists did not differ in our study. Further, there was not much difference in percentages of gap specialist (pioneer) and generalist (shade-tolerant) species that produce dormant seeds (MPD + PD + PY): 6 of 13 (46%) for gap specialists and 8 of 19 (42%) for generalists (Fig. 2b).

Dormancy is the main mechanism controlling germination in the late rainy season, where PD is more common than other dormancy classes, and the delay of germination is longer than in the dry and early rainy seasons. In the dry season, when both dispersal and dormancy appear to have the same relative importance in controlling germination time, the number of species with ND seeds almost equals that of species with dormant seeds, and PY appears to be slightly favoured (40%) within dormancy classes. In the early dry season, dispersal timing is the main mechanism that controls germination, and ND seeds are favoured. Garwood (1983) considered both timing of dispersal and dormancy to be part of a drought-avoidance syndrome (Angevine and Chabot, 1979). Nevertheless, seed dormancy class might not be related to control of germination time. Seed germination does not need to occur at the optimal time for seedling establishment if selection on other stages of the life cycle, such as pollination, seed development and seed dispersal, are relatively more severe (Garwood, 1986). Moreover, it was suggested that drought tolerance traits could be more common than suspected, as was reported for seedlings of *Licania platypus* on Barro Colorado Island (Tyree *et al.*, 2002).

Overall, our results show only a small increase in the proportion of species with dormant seeds as precipitation decreases, which agrees with those of Baskin and Baskin (2005). In the wettest zone of the gradient, 57% of the species are non-dormant, and the proportion only declines to 53% in the driest zone. These numbers are nearly identical to those given by Baskin and Baskin (2005) for rainforest and tropical semi-evergreen forest (58 and 52%, respectively). The proportion of species with PD is similar throughout much of the precipitation gradient (27–29%), but it declines to 21% in the driest zone. The proportion of species with MD is nearly constant, and it is never important. The proportion of species with MPD increases with a decrease in precipitation, from 6.3 to 9.4%. PY is the only class of dormancy that shows a significant trend to increase with a decrease in precipitation, from 8% in the wettest zone to 15% in the driest zone.

Acknowledgements

The authors thank Jorge Aranda for collecting seeds for the first 2 years of the study; Rolando Pérez and

Salomón Aguilar for providing information about seed trees, timing of fruit maturity and fruit characteristics; Suzanne Loo de Lao for statistical advice; and Mark Wishnie for helping make arrangements for the first author to take a 2-year leave of absence from the Smithsonian Tropical Research Institute to attend graduate school at the University of Kentucky. This paper is a scientific contribution of the Native Species Reforestation Project (PRORENA), a collaborative research effort led by the Center for Tropical Forest Science of the Smithsonian Tropical Research Institute and the Yale School of Forestry and Environmental Studies. Financial support was given by FIDECO (Fundacion Natura), the Center for Tropical Forest Science Research Grant Program, and OAS-Fulbright and University of Kentucky fellowships.

References

- Acuña, P.I. and Garwood, N.C. (1987) Efecto de la luz y la escarificación en las semillas de cinco especies de árboles secundarios. *Revista de Biología Tropical* **35**, 203–207.
- Almeida, M.J.B., Ferraz, I.D.K. and Bassin, F. (1999) Estudos sobre a permeabilidade do tegumento e a geminação de sementes de *Hymenaea courbaril* L. (Caesalpinaceae), uma espécie de uso múltiplo. *Revista da Universidade do Amazonas: Série Ciências Agrárias, Manaus* **8** (1–2), 63–71.
- Alvarez-Buylla, E.R. and Martínez-Ramos, M. (1992) Demography and allometry of *Cecropia obtusifolia*, a neotropical pioneer tree – an evaluation of the climax-pioneer paradigm for tropical rainforests. *Journal of Ecology* **80**, 275–290.
- Angevine, M.W. and Chabot, B.F. (1979) Seed germination syndromes in higher plants. pp. 188–206 in Solbrig, O.T.; Jain, S.; Johnson, G.B.; Raven, P.H. (Eds) *Topics in plant population biology*. New York, Columbia University Press.
- Angiosperm Phylogeny Group (2003) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. *Botanical Journal of the Linnean Society* **141**, 399–436.
- Baskin, C.C. and Baskin, J.M. (1998) *Seeds: Ecology, biogeography and evolution of dormancy and germination*. San Diego, Academic Press.
- Baskin, C.C. and Baskin, J.M. (2005) Seed dormancy in trees of climax tropical vegetation types. *Tropical Ecology* **46**, 17–28.
- Baskin, J.M. and Baskin, C.C. (2003) Classification, biogeography, and phylogenetic relationships of seed dormancy. pp. 517–544 in Smith, R.D.; Dickie, J.B.; Linnington, S.H.; Pritchard, H.W.; Probert, R.J. (Eds) *Seed conservation: Turning science into practice*. Kew, Royal Botanic Gardens.
- Baskin, J.M. and Baskin, C.C. (2004) A classification system for seed dormancy. *Seed Science Research* **14**, 1–16.
- Baskin, J.M., Baskin, C.C. and Li, X. (2000) Taxonomy, anatomy and evolution of physical dormancy in seeds. *Plant Species Biology* **15**, 139–152.
- Baskin, J.M., Baskin, C.C. and Dixon, K.W. (2006) Physical dormancy in the endemic Australian genus *Stylobasium*,

- a first report for the family *Surianaceae* (*Fabales*). *Seed Science Research* **16**, 229–232.
- Brahmam, M.** (1996) Effect of pre-sowing treatments for hastening the germination of *Enterolobium cyclocarpum* (Jacq.) Griseb. and *Hymenaea courbaril* L. *Indian Forester* **122**, 740–745.
- Brahmam, M., Sree, A. and Saxena, C.** (1996) Effect of pre-sowing treatments on the seed germination of *Sapindus mukorossi* Gaertn. and *Sapindus trifoliatus* L. (*Sapindaceae*). *Advances in Plant Science* **9**, 137–142.
- Condit, R.** (1998) Ecological implications of changes in drought patterns: Shifts in forest composition in Panama. *Climatic Change* **39**, 413–427.
- Condit, R., Hubbell, S.P. and Foster, R.B.** (1996a) Changes in tree species abundance in a Neotropical forest: Impact of climatic change. *Journal of Tropical Ecology* **12**, 231–256.
- Condit, R., Hubbell, S.P. and Foster, R.B.** (1996b) Assessing the response of plant functional types to climatic change in tropical forests. *Journal of Vegetation Science* **7**, 405–416.
- Condit, R., Robinson, W.D., Ibáñez, R., Aguilar, S., Sanjurjo, A., Martínez, R., Stallard, R.F., García, T., Angehr, G.R., Petit, L., Wright, S.J., Robinson, T.R. and Heckadon, S.** (2001) The status of the Panama Canal Watershed and its biodiversity at the beginning of the 21st century. *BioScience* **51**, 389–398.
- Condit, R., Aguilar, S., Hernandez, A., Perez, R., Lao, S., Angehr, G., Hubbell, S.P. and Foster, R.B.** (2004) Tropical forest dynamics across a rainfall gradient and the impact of an El Niño dry season. *Journal of Tropical Ecology* **20**, 51–72.
- Correa, A., M.D.** (2003) *Byrsonima crassifolia* (L.) Kunth. pp. 342–345 in Vozzo, J.A. (Ed.) *Tropical tree seed manual*. Agriculture Handbook Number 721. Washington, DC, United States Department of Agriculture, Forest Service.
- Dalling, J.W., Swaine, M.D. and Garwood, N.C.** (1997) Soil seed bank community dynamics in seasonally moist lowland tropical forest, Panama. *Journal of Tropical Ecology* **13**, 659–680.
- D'Arcy, W.G.** (1987) *Flora of Panama. Part I. Introduction and checklist*. St. Louis, Missouri Botanical Garden.
- Daws, M.I., Orr, D., Burslem, D.F.R.P. and Mullins, C.E.** (2006) The effect of high temperature on chalazal plug removal and germination of *Apeiba tibourbou* Aubl. *Seed Science and Technology* **34**, 221–225.
- Ferraz, I.D.K., Filho, N.L., Imakawa, A.M., Varela, V.P. and Piña-Rodrigues, F.C.M.** (2004) Características básicas para um agrupamento ecológico preliminar de espécies madeireiras da floresta de terra firme da Amazônia Central. *Acta Amazonica* **34**, 621–633.
- Flores, E.M.** (2002) *Pseudosamanea guachapele* (Kunth) Harms. pp. 666–669 in Vozzo, J.A. (Ed.) *Tropical tree seed manual*. Agriculture Handbook Number 721. Washington, DC, United States Department of Agriculture, Forest Service.
- Flores, E.M., Rivera, D.I. and Vazquez, N.M.** (1986) Germinación y desarrollo de la plántula de *Cassia grandis* L. (*Caesalpinioideae*). *Revista de Biología Tropical* **34**, 289–296.
- Garwood, N.C.** (1983) Seed germination in a seasonal tropical forest in Panama: A community study. *Ecological Monographs* **53**, 159–181.
- Garwood, N.C.** (1986) Constraints on the timing of seed germination in a tropical forest. pp. 347–355 in Estrada, A.; Fleming, T.H. (Eds) *Frugivores and seed dispersal*. Dordrecht, W. Junk Publishers.
- Geilfus, F.** (1994) *El Árbol al servicio del Agricultor*. Turrialba, Costa Rica, Guía de especies CATIE.
- Gill, L.S. and Bamidele, J.F.** (1981) Seed morphology, germination and cytology of three savanna trees of Nigeria. *Nigerian Journal of Forestry* **11**, 16–23.
- Grushvitzky, I.V.** (1967) After-ripening of seeds of primitive tribes of angiosperms, conditions and peculiarities. pp. 329–336 + figures 1–8. in Borris, H. (Ed.) *Physiologie, ökologie und biochemie der keimung*. Griefswald, Germany, Ernst-Moritz-Arndt-Universität.
- Holdridge, L.R.** (1967) *Life zone ecology*. San José, Costa Rica, Tropical Science Center.
- Hubbell, S.P. and Foster, R.B.** (1986) Commonness and rarity in a Neotropical forest: Implications for tropical tree conservation. pp. 205–231 in Soule, M.E. (Ed.) *Conservation biology: The science of scarcity and diversity*. Sunderland, Massachusetts, Sinauer Associates.
- Knight, D.H.** (1975) A phytosociological analysis of species-rich tropical forest on Barro Colorado Island, Panama. *Ecological Monographs* **45**, 259–284.
- Marin, W.A. and Flores, E.M.** (2002a) *Copaifera aromatica* Dwyer. pp. 405–407 in Vozzo, J.A. (Ed.) *Tropical tree seed manual*. Agriculture Handbook Number 721. Washington, DC, United States Department of Agriculture, Forest Service.
- Marin, W.A. and Flores, E.M.** (2002b) *Copaifera camibar*. pp. 408–410 in Vozzo, J.A. (Ed.) *Tropical tree seed manual*. Agriculture Handbook Number 721. Washington, DC, United States Department of Agriculture, Forest Service.
- Munson, R.H.** (1984) Germination of western soapberry as affected by scarification and stratification. *HortScience* **19**, 712–713.
- Naidu, C.V., Rajendrudu, G. and Swamy, P.M.** (1999) Effect of temperature and acid scarification on seed germination of *Sapindus trifoliatus* Vahl. *Seed Science and Technology* **27**, 885–892.
- Naidu, C.V., Rajendrudu, G. and Swamy, P.M.** (2000) Effect of plant growth regulators on seed germination of *Sapindus trifoliatus* Vahl. *Seed Science and Technology* **28**, 249–252.
- Negi, A.K. and Todaria, N.P.** (1993) Improvement of germination of some Himalayan tree seeds by temperature treatment. *Seed Science and Technology* **21**, 675–678.
- Nikolaeva, M.G.** (1977) Factors controlling the seed dormancy pattern. pp. 51–74 in Khan, A.A. (Ed.) *The physiology and biochemistry of seed dormancy and germination*. Amsterdam, North Holland.
- Nikolaeva, M.G., Rasumova, M.V. and Gladkova, L.M.** (1985) *Reference book on dormant seed germination*. Danilova, M.F. (Ed.) Leningrad, 'Nauka' Publishers (in Russian).
- Pearson, T.R.H., Burslem, D.F.R.P., Mullins, C.E. and Dalling, J.W.** (2002) Germination ecology of neotropical pioneers: Interacting effects of environmental conditions and seed size. *Ecology* **83**, 2798–2807.
- Piña-Rodrigues, F.C.M. and Figliolia, M.B.** (2005) Embryo immaturity associated with delayed germination in recalcitrant seeds of *Virola surinamensis* (Rol.) Warb. (*Myristicaceae*). *Seed Science and Technology* **33**, 375–386.

- Pritchard, H.W., Haye, A.J., Wright, W.J. and Steadman, K.J.** (1995) A comparative study of seed viability of *Inga* species: Desiccation tolerance in relation to the physical characteristics and chemical composition of the embryo. *Seed Science and Technology* **23**, 85–100.
- Pyke, C.R., Condit, R., Aguilar, S. and Lao, S.** (2001) Floristic composition across a climatic gradient in a neotropical lowland forest. *Journal of Vegetation Science* **12**, 553–566.
- Ramalho Carvalho, P.** (1994) *Espécies florestais Brasileiras. Recomendações silviculturais, potencialidades e uso da Madeira*. Brasil, Empresa Brasileira de Pesquisa Agropecuária. Centro Nacional de Pesquisa de Florestas (EMBRAPA-CNPQ).
- Salazar, R.** (2000) *Manejo de semillas de 100 especies forestales de América Latina, Vol. 1*. CATIE. Proyecto de semillas forestales. Turrialba. Costa Rica, Danida Forest Seed Centre.
- Sandi, C. and Flores, E.M.** (2002) *Prioria copaifera* Grieseb. pp. 654–656 in Vozzo, J.A. (Ed.) *Tropical tree seed manual*. Agriculture Handbook Number 721. Washington, DC, United States Department of Agriculture, Forest Service.
- Santiago, L.S., Kitajima, K., Wright, S.J. and Mulkey, S.S.** (2004) Coordinated changes in photosynthesis, water relations and leaf nutritional traits of canopy trees along a precipitation gradient in lowland tropical forest. *Oecologia* **139**, 495–502.
- Sautu, A.** (2004) Ecology, morphology, and germination physiology of tree seeds in a tropical semievergreen forest in the Panama Canal Watershed, with special reference to seed dormancy classes along a precipitation gradient. M.S. thesis, University of Kentucky, Lexington.
- Sautu, A., Baskin, J.M., Baskin, C.C. and Condit, R.** (2006) Studies on the seed biology of 100 native species of trees in a seasonal moist tropical forest, Panama, Central America. *Forest Ecology and Management* **234**, 245–263.
- Swaine, M.D. and Whitmore, T.C.** (1988) On the definition of ecological species groups in tropical rain forests. *Vegetatio* **75**, 81–86.
- Tosi, J.A.** (1971) *Zonas de vida, una base ecológica para investigaciones silvícolas y inventariación forestal en la República de Panamá*. Rome, Organización de las Naciones Unidas para Agricultura y Alimentación.
- Tweddle, J.C., Dickie, J.B., Baskin, C.C. and Baskin, J.M.** (2003) Ecological aspects of seed desiccation sensitivity. *Journal of Ecology* **91**, 294–304.
- Tyree, M.T., Vargas, G., Engelbrecht, B.M.J. and Kursar, T.A.** (2002) Drought until death do us part: A case study of the desiccation-tolerance of a tropical moist forest seedling-tree, *Licania platypus* (Hemsl.) Fritsch. *Journal of Experimental Botany* **53**, 2239–2247.
- Vázquez-Yañez, C.** (1974) Studies on the germination of seeds of *Ochroma lagopus* Swartz. *Turrialba* **24**, 176–179.
- Vázquez-Yañez, C. and Perez-García, B.** (1976) Notas sobre la morfología y la anatomía de la testa de las semillas de *Ochroma lagopus* Sw. *Turrialba* **26**, 310–311.
- Vega, C., Patiño, F. and Rodríguez, A.A.** (1983) *Viabilidad de semillas en 72 especies forestales tropicales almacenadas al medio ambiente*. Tomo II. Quintana Roo, México, Instituto de Investigaciones Forestales.
- Vora, R.S.** (1989) Seed germination characteristics of selected native plants of the lower Rio Grande Valley, Texas. *Journal of Range Management* **42**, 36–40.
- Whitmore, T.C.** (1989) Canopy gaps and the two major groups of forest trees. *Ecology* **70**, 536–538.

Received 20 July 2006
 accepted after revision 19 February 2007
 © 2007 Cambridge University Press