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Diversity of embryos and seed dormancy in Rubiaceae: a taxonomic/phylogenetic and biogeographic perspective

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Abstract

We have reviewed seed dormancy and germination in the Rubiaceae, the fourth-largest angiosperm family (in terms of species richness), in relation to ecology, life form, biogeography and phylogeny (subfamily/tribe). Life forms include trees, shrubs, vines and herbs, and tropical rainforest trees have the greatest number of tribes and species. The family has five kinds of embryos: investing, linear-full, linear-underdeveloped, spatulate and spatulate-underdeveloped, and seeds are non-dormant (ND) or have morphological (MD), morphophysiological (MPD) or physiological (PD) dormancy. Except for the occurrence of the investing embryo only in dry fruits of Dialypetalanthoideae, each kind of embryo is found in dry and fleshy fruits of Dialypetalanthodies and of Rubioideae. In tropical and temperate regions, there are species with ND seeds and others whose seeds have MD, MPD or PD. A complete seed dormancy profile (i.e. some species with ND seeds and others whose seeds have MD, MPD or PD) was found for tropical rainforest trees and shrubs and semi-evergreen rainforest shrubs. Dormancy-break occurs during cold or warm stratification or dry-afterripening, depending on the species. Some tropical species have long periods of dormancy-break/germination extending for 4–5 to 30–40 weeks. Soil seed banks are found in 5 and 15 tribes of Rubiaceae in tropical and temperate regions, respectively. With increased distance from the Equator, diversity of life forms and seed dormancy decreases, resulting in only herbs with PD at high latitudes. We conclude that the low species richness of Rubiaceae in temperate regions is not related to low diversity of seed dormancy/germination.

Introduction

The Rubiaceae consists of two subfamilies (Dialpetalanthoidea and Rubioideae) (Razafimandimbison and Rydin, 2024), 620 genera (Plants of World Online) and 13,465 species (Stevens 2001). It is the fourth-largest angiosperm family after Asteraceae, Orchidaceae and Fabaceae (Mabberley, 2017). Most species of Rubiaceae grow in tropical and subtropical regions, especially in non-disturbed lowland moist forests, and members of this family may be the most species-abundant woody plants present in the forest (Davis et al., 2009). For example, in the rainforest flora of peninsular Malaysia, the families with 20 or more genera are Annonaceae, Euphorbiaceae, Fabaceae and Rubiaceae with 25, 57, 27 and 24 genera, respectively, and with 130, 344, 127 and 237 species, respectively (Ng, 1988). Some species in a few tribes grow in high latitude/elevation habitats, including subpolar regions of the Arctic and Antarctic but not on the Antarctic continent (Davis et al., 2009). With an increase in latitude, the number of tribes and genera represented in the flora decreases. For example, Gleason and Cronquist (1991) included nine genera in four tribes (Michelleae, Naucleae, Rubieae and Spermacoceae) in the flora of northeastern USA and adjacent Canada, but Hultén (1968) has only the genus *Galium* (Rubieae) in the flora of Alaska and neighbouring Canadian territories.

Although studies have been conducted on seed dormancy and germination of many species of Rubiaceae (Baskin and Baskin, 2014), no global assessment of the ecology and biogeography of seed dormancy or of the phylogenetic relationships of species with non-dormant (ND) seeds and those with different kinds (classes) of dormancy is available for the family. However, an analysis of the geographical distribution, diversity, endemism and on-going taxonomic work for the Rubiaceae has been published by Davis et al. (2009). The purpose of our review is to consider seed dormancy/germination of the Rubiaceae in relation to embryo morphology, ND and classes of dormancy, seed ecology, plant life form, biogeography/vegetation zone and phylogeny (tribe). We addressed five questions. (1) Do embryo morphology and seed dormancy vary in the two subfamilies of Rubiaceae? (2) What is the seed dormancy profile (i.e. proportion of ND and the different classes of dormancy) of Rubiaceae for the major vegetation zones on earth and for the various life forms in this family? (3) Does the morphology of Rubiaceae flowers (e.g. bisexual, dioecious, distyly and homostyly) have an influence of seed dormancy/germination? (4) How is seed dormancy broken in Rubiaceae? (5) What life forms and tribes of Rubiaceae are the most likely ones to form soil seed banks? Before addressing these questions, a family overview and background information on palaeohistory, seeds, embryo morphology and seed dormancy in the Rubiaceae will be provided.

Family overview

According to Davis et al. (2009), the five most species-rich countries/regions for Rubiaceae are Columbia, Venezuela, New Guinea, Brazil (north) and the Democratic Republic of the Congo. At least 30 genera of Rubiaceae have 100 or more species, and *Psychotria* has 1834 species, making it the world's third largest angiosperm genus after *Astragalus* (Fabaceae) with 3200 species and *Bulbophyllum* (Orchidaceae) with *c.* 2000 species (Frodin, 2004; Plants of World Online). However, the Rubiaceae has *c.* 200 monotypic genera, *c.* 330 genera with only 2–3 species and *c.* 450 genera with 4–10 species (Davis et al., 2009). Based on 13,143 species of Rubiaceae, Davis et al. (2009) estimated that 64% of them are endemic to a particular island/country; the five places with the highest number of endemics are New Guinea, Madagascar, Philippines, Borneo and Cuba with 620, 520, 443, 428 and 344 endemic species, respectively.

Life forms of Rubiaceae are trees, shrubs, vines/lianas/climbers and herbs, including epiphytes. Tree height ranges from *c.* 10 to 30 m (Robbrecht, 1988; Gardner et al., 2000; Ricker et al., 2013) with one of the tallest trees, *Blepharidium guatemalense*, reaching a height of 40 m (Ricker et al., 2013). In contrast, small pachycaul (few branches) treelets such as *Maschalodesme* in New Guinea are only 1–2 m tall (Ridsdale et al., 1972). There are 32 genera of climbers in the Rubiaceae in the Neotropics (Delprete, 2022a) and 88 in the Old World, including Eurasia, Africa and the West Malay Archipelago (Hu and Li, 2015). Plants of Rubiaceae climb via stipules, hook-like or straight thorns, involucral bracts, adventitious roots or twining stems (Robbrecht, 1988; Delprete, 2022a).

Benzing (1991) reported 85 species of epiphytic Rubiaceae. Members of the genera *Anthorrhiza*, *Hydnophytum*, *Myrmedodia*, *Myrmephytum* and *Squamellaria* in subtribe Hydnophytinae of tribe Pychotrieae are not only epiphytic, but the hypocotyl of the seedling enlarges to form a tuber with chambers that become occupied by ants (Huxley, 1978; Jebb, 1991). These ant-plants are distributed throughout southeast Asia, being most diverse in New Guinea, (Huxley, 1978; Huxley and Jebb, 1991; Chomicki and Renner, 2016, 2017), and species of *Hydnophytum* and *Myrmecodia* occur in northern Australia (Huxley, 1982). Plants of *Hydnophytum formicarum*, *H. moseleyanum*, *Myrmecodia armata* and *M. tuberosa* are succulent (Succulent Plants Website).

Herbaceous Rubiaceae are annuals or perennials, and genera such as *Borreria*, *Diodia*, *Galianthe*, *Galium*, *Hexasepalum*, *Mitracarpus*, *Paederia*, *Richardia* and *Spermacoce* can be invasive and even serious weeds in crops (Salamero et al., 1997; Mersereau and DiTommaso, 2003; Gallon et al., 2018; Kalsing et al., 2020). Some species of *Richardia* and *Spermacoce* have become resistant to the herbicide glyphosate used to control weeds in crops such as soybeans (Kalsing et al., 2020). The Rubiaceae also includes the mangrove shrubs *Rustia occidentalis* and *Scyphiphora hydrophyllacea* (Tomlinson, 1986). Further, species of a few genera such as *Durringtonia* (Henderson and Guymer, 1985), *Limnosipanea* (Delprete and Cortés-B, 2004) and *Oldenlandia* (Mukherjee and Ghosh, 2015) grow in wet habitats.

Taxonomic descriptions of species of Rubiaceae may include information about raphids (calcium oxalate crystals), leaves, inflorescences, flowers, fruits and seeds (Dwyer, 1980; Robbrecht, 1988; Kirkbride et al., 2000; Simpson, 2006; Mabberley, 2017). Raphides are present in Rubioideae, but they may, or may not, be present in Dialypetalanthoideae. Leaves are entire and simple, and they are opposite or decussate (rarely whorled) on the stem. Leaves of some species, for example *Tricalysia*, have domatia used by ants. Stipules are entire, bifid or fimbriate and may be deciduous or persistent. They are either intrapetiolar (stipule on both sides of a leaf fuse, placing margin of stipule between stem and petiole) or interpetiolar (stipules of opposite leaves fuse, placing margin of stipulate on stem between the petioles of opposite leaves). In some species, the stipules have colleters (glands) that produce mucilage.

Flowers are usually produced in a cyme, but sometimes they are solitary or in panicles or heads. The calyx has four or five sepals that fuse, forming a tube with distinct lobes, and the four or five (or more) petals fuse, forming a tubular actinomorphic flower with lobes. Flowers have four or five (rarely 8–10) stamens that dehisce pollen via longitudinal slits, but stamens of some species have pores. The ovary is inferior (or rarely half inferior) and has 1–10 locules, often 2, with 1 to many ovules per locule. The fruit is a berry, capsule, drupe or schizocarp with 1, 2–9, 10–24, 25–49 or ≥50 endospermous seeds, depending on the species and kind of fruit produced.

Family palaeohistory

In a critical analysis of 134 fossil specimens (macrofossils and pollen) attributed to the Rubiaceae, Graham (2009) accepted the genus name of 43 of them as being correct, but he questioned the identification of the other 91 specimens. The oldest accepted fossils for Rubiaceae were: Dialypetalanthoideae, Eocene to Pliocene from Australia and Middle Eocene from Oregon (USA) and Rubioideae, Late Eocene from Panama. The presence of fossils of the two subfamilies of Rubiaceae in the Eocene and their wide distribution in the world suggested to Graham that the family originated in the Late Cretaceous or Paleocene. Accepted fossils of Rubiaceae from the Eocene have been collected in Argentina, Australia, Caribbean region, Panama and the USA (Kentucky/Tennessee, Mississippi/Tennessee and Oregon/Washington). Based on fossils of 20 accepted genera from the Miocene collected in Africa, Central America, Europe, North America, South America and south-eastern Pacific-Asia, Graham concluded that the Miocene was a period of great diversification of the Rubiaceae.

The Rubiaceae is predominantly pantropical in distribution. According to Delprete and Jardin (2012), about one-third of the genera and one-half of the species in this family occur in the neotropics. In South America, the Rubiaceae is especially diverse in the Amazon Basin, but members of this family are also found in cloud forests and Páramo of the Andes, savannas (cerrado), dry forests (caatinga and restinga), Atlantic forest of Brazil and llanos (seasonally flooded areas) of Brazil and Venezuela (Delprete and Jardin, 2012). Palaeobotanical research, for example palynology, in the neotropics has revealed that a significant increase in plant diversity occurred in northern South America in the early to middle Eocene (Jaramillo et al., 2006, 2010). Thus, by the Eocene, diverse rainforests were present in South America (Burnham and Johnson, 2004). This increase in plant diversity, mostly angiosperms, occurred during a period of rapid global warming at the Paleocene–Eocene boundary, that is the Paleocene–Eocene Thermal Maximum (PETM), which was correlated with thousands of petagrams (10^{15} g) of carbon being released into the atmosphere (McInerney and Wing, 2011). During the PETM, the 5–8°C increase in global temperature apparently promoted the rapid diversification of angiosperm species and thus greatly increased plant species richness of Neotropical forests (Dick and Pennington, 2019). However, tropical dry forests did not develop until the late Eocene, and other types of tropical vegetation, for example savanna, montane forest and Páramo, did not appear until the Miocene or Pliocene, after the PETM (Jaramillo, 2023). We note that the research cited here does not provide specific information about speciation of the Rubiaceae in the neotropics; however, it does provide clues as to when significant species diversification may have occurred in the Rubiaceae of South America.

Based on molecular data, various dates have been proposed for the beginning of divergence of Rubiaceae, for example 66.1 Ma (Antonelli et al., 2009) to 84.9 Ma (Manns et al., 2012) and 90.4 Ma (Bremer and Eriksson, 2009). Bremer et al. (2004) obtained a stem age of 108 Ma for the Gentianales. However, when Wikström et al. (2015) reanalysed the dataset of Bremer et al. (2004) and added information from DNA analysis of 67 additional taxa of Rubiaceae, they obtained a stem and crown age for Gentianales of 99 and 75 Ma, respectively. Using the combined dataset, Wikström et al. (2015) obtained an estimated age for the Rubiaceae of 87 Ma with a credibility interval of 78–96 Ma.

Antonelli et al. (2009) concluded that the Rubiaceae originated in the palaeotropics in the Early Paleocene and that members of the family reached North America in the Late Paleocene/Early Eocene via land bridges such as the North Atlantic Thulean Land Bridge. From North America, Rubiaceae migrated to South America. In contrast, Manns et al. (2012) concluded that the ancestor of the Dialypetalanthoideae was present in South America during the Late Cretaceous and that they were dispersed to Central America in the Early Paleocene and to islands in the Caribbean in the Oligocene–Miocene.

Much research using molecular techniques has been conducted to determine the general phylogenetic relationships in the Rubiaceae. Consequently, we have a good understanding of the phylogenetic relations of the Rubiaceae at the whole family level (Robbrecht and Manen, 2006; Davis et al., 2007; Bremer and Eriksson, 2009; Rydin et al., 2009, 2017; Wikström et al., 2015, 2020; Razafimandimbison and Rydin, 2024). Also, the phylogenetic relationships within the subfamilies (Andreasen and Bremer, 2000; Bremer and Manen, 2000; Sonké et al., 2008; Manns and Bremer, 2010; Wen and Wang, 2012; Kainulainen et al., 2013; Thureborn et al., 2022 Razafimandimbison and Rydin, 2024) and various tribes (e.g. Bremer and Thulin, 1998; Rova et al., 2002; Paudyal et al., 2014; Razafimandimbison et al., 2014, 2022; Delprete, 2015; Santos et al., 2021) have been explored. However, questions remain about the phylogenetic relationships within the Rubiaceae. For example, the Acranthereae, Coptosapelteae and Lucelieae remain unplaced in the Rubiaceae (Bremer and Eriksson, 2009; Manns et al., 2012; Wikström et al., 2020; Razafimandimbison and Rydin, 2024).

Molecular phylogenetic studies have revealed much information about the dispersal and diversification of the Rubiaceae. Tribe Rubieae is thought to have originated in the Old World, after which it was dispersed to the New World (Soza and Olmstead, 2010; Ehrendorfer et al., 2018). Janssens et al. (2016) concluded that Spermacoceae originated in the Late Eocene and diversified during the Oligocene and Miocene. These authors attributed the presence of two clades of Spermacoceae in Madagascar to long-distance dispersal events from eastern tropical Africa and from tropical America in the Oligocene and radiation in the Miocene. The ancestor of the genera *Colletoecema* and *Seychellea* likely reached the Seychelles islands from Africa via bird dispersal, and the two genera diverged in the late Oligocene–Early Pliocene (Razafimandimbison et al., 2020). Diversification and dispersal of *Plocama* occurred in the Early Miocene during a time of climate warming. Today, there are sister species of *Plocama* growing in the Canary Islands and in eastern and southern Africa (Rincón-Barrado et al., 2021).

Deng et al. (2017) reconstructed the evolution and migration of *Theligonum* and *Kelloggia*, which originated from ancestors growing in tropical/subtropical habitats along the coast of the Tethys Sea. When the Tibetan Plateau formed, it separated the eastern and western parts of the Tethys region, which helps to explain the current distribution of *Theligonum* in Asia and in the Mediterranean/Near East. The Plateau also separated the distribution of *Kelloggia* into an eastern and western part. The occurrence of *Kelloggia* in alpine meadows on the Tibetan Plateau represents the western part of this ancient distribution pattern; the eastern part *per se* became extinct. However, *Kelloggia* (from the western part of the distribution) migrated to North America via the North Atlantic Land Bridge and now grows in coniferous forests on the West Coast (Nie et al., 2005; Deng et al., 2017).

The ancestral lineage of the Psychotrieae alliance has been inferred to have originated in Africa in the Upper Cretaceous (Razafimandimbison et al., 2017), and after its dispersal to the neotropics tribes Gaertnereae, Morindeae and Palicoureeae were formed. The alliance was dispersed from the neotropics to Asia and the Pacific islands, and in the Pacific, it gave rise to tribe Psychotrieae. During the last 10 million years, the alliance has reached the Western Indian Ocean Region at least 14 times via dispersal events from Africa, Asia and the Pacific. According to Barrabé et al. (2014), New Caledonia has been colonized four times by *Psychotria* and allied genera, but only one clade of *Psychotria s.l.* underwent extensive and rapid diversification, resulting in 85 species that are all endemic to New Caledonia.

Molecular phylogenetic studies also have provided insight on long-distance dispersal and speciation within the Rubiaceae. For example, the Coffeeae alliance has undergone many dispersal events in the Western Indian Ocean Region, followed by diversification upon arrival in new habitats. Kainulainen et al. (2017) have inferred at least 15 immigrations of the Coffeeae alliance into Madagascar in the last 10 million years, with many of the dispersal events originating in Africa. Further, Madagascar has been the source of dispersal of members of the Coffeeae alliance to the Comoros, Mascarenes and Seychelles islands.

Various kinds of studies have been done with the aim of gaining insight into species diversification of Rubiaceae. Ploidy levels (2×, 4×, 6×, 7× and 10×) in the New Zealand species of *Coprosma* were evaluated to test the hypothesis that species with high ploidy levels occur in more biomes (i.e. types of habitat) than those with low ploidy levels (Liddell et al., 2021). Species with high ploidy were three to eight times more likely to occur in more than one biome than those with low ploidy. The authors suggested that whole-genome duplication has promoted expansion into additional biomes and thus speciation.

Niche modelling, *in lieu* of transplant studies, was used to investigate the role of ecogeographic (i.e. ecology and geography) isolation as a reproductive barrier in section *Amphiotis* of *Houstonia* (Glennon et al., 2012). Diploid and tetraploid forms of *H. longifolia* exhibited some ecogeographic isolation, but those of *H. purpurea* did not. The authors suggested that ecogeographic isolation has played a role in species divergence of *Houstonia* because niche models and principal components analyses showed that the species have niches with different climatic variables. Further, species diversification of the diploid-polyploid *Galium pusillum* complex has occurred in northern Europe in areas covered by glaciers during the Pleistocene (Kolář et al., 2013). Studies on niche differentiation of different species and ploidy levels of the *G. pusillum* complex in the deglaciated area revealed high levels of ecogeographic segregation/isolation.

Seeds of Rubiaceae

Seeds vary from <1 mm (dust-like or minute) to 10–20 mm long, and those of some species are distinguished by presence of wings or trichomes. The embryo is differentiated and has two cotyledons that are wider than, or the same width as, the hypocotyl-radicle, depending on the species. Also, embryo length relative to seed length varies with the species (e.g. Martin, 1946). The endosperm in seeds of Rubiaceae may, or may not, contain starch, but it does contain hemicellulose and galactomannans (Jacobsen, 1984; Robbrecht, 1988). In tribes Guettardeae, Morindeae and Vanguerieae, the endosperm is soft and contains oil. However, Robbrecht (1988) observed that the hard endosperm in seeds of *Psychotria* also contains some oil and suggested that presence of oil in the endosperm is not a dependable taxonomic character. Depending on the species, the endosperm is soft, fleshy, fleshy-firm, hard or cartilaginous (Robbrecht, 1988). The endosperm may have shallow or deep rumination, which provides useful taxonomic information for a few genera.

The seed coat of Rubiaceae is not multiplicative and generally consists of only the outer epidermis and a few layers of mesophyll cells. Depending on the genus, cells of the seed coat may be thin walled or variously thickened/lignified (Corner, 1976). In some Rubiaceae, the integuments are well formed, but in other species, the integuments may be absorbed during seed development resulting in seeds without a seed coat (Boesewinkel and Bouman, 1984). The seed coat does not have a water-impermeable palisade layer of cells (macrosclereids). Thus, the Rubiaceae is not included on the list of plant families whose seeds have physical or combinaltional (physical + physiological) dormancy (Baskin and Baskin, 2014).

Only a relatively few species of Rubiaceae have been reported to have recalcitrant (desiccation-sensitive) seed storage behaviour, and all these species are trees or shrubs (Table 1). Seeds of some

Table 1. Species of Rubiaceae whose seeds have recalcitrant (R) or intermediate (I) seed storage behaviour

Species	Storage	Tribe	Life form	References
Alibertia patinoi	R	Cordiereae	Tree	Escobar and Torres (2013) and Ley-López et al. (2023)
Alibertia sorbilis	R	Cordiereae	Tree	Braga et al. (1999)
Atractocarpus chartaceus	R	Gardenieae	Tree	Hamilton et al. (2013)
Atractocarpus fitzalanii	R	Gardenieae	Shrub or tree	Hamilton et al. (2013)
Atractocarpus stipularis	R	Gardenieae	Tree	Hamilton et al. (2013)
Atractocarpus vaginatus	I	Gardenieae	Shrub or tree	Hong et al. (1998)
Coffee arabica	I	Coffeeae	Tree	Ellis et al. (1990)
Coffea canephora	I	Coffeeae	Tree	Hong et al. (1998), Dussert et al. (1999) and Oryem-Origa (1999)
Coffea liberica	R	Coffeeae	Tree	Hong and Ellis (1995) and Hong et al. (1998)
Coffea racemosa	I	Coffeeae	Shrub	Hong et al. (1998)
Coussarea paniculata	R	Coussareeae	Shrub or tree	Ley-López et al. (2023)
Faramea occidentalis	R	Coussareeae	Shrub or tree	Ley-López et al. (2023)
Faramea tamberlikiana	R	Coussareeae	Shrub or tree	Ley-López et al. (2023)
Fosbergia shweliensis	I	Gardenieae	Tree	Li et al. (2013)
Genipa americana	I	Gardenieae	Tree	Magistrali et al. (2013)
Gynochthodes jasminoides	I	Morindeae	Climber	Sommerville et al. (2021)
Isertia haenkeana	R	Isertieae	Tree	Ley-López et al. (2023)
Ixora brevifolia	R	Ixoreae	Tree	José et al. (2007)
Ixora nicaraguensis	R	Ixoreae	Shrub or tree	Ley-López et al. (2023)
Ixora smeruensis	R	Ixoreae	Shrub	Darmayanti et al. (2020)
Posoqueria latifolia	R	Posoquerieae	Shrub or tree	Ley-López et al. (2023)
Psychotria simmondsiana	I	Psychotrieae	Shrub or tree	Sommerville et al. (2021)
Tocoyena pittieri	R	Gardenieae	Shrub or tree	Ley-López et al. (2023)

Coffea species, *Fosbergia shweliensis*, *Genipa americana*, *Gynochthodes jasminoides* and *Psychotria simmondsiana* have been reported to have intermediate storage behaviour. Further, seeds of *Coprosma*, *Gardenia*, *Kadua* and *Psydrax* from Hawaii are sensitive to freezing (Chau et al., 2019), suggesting that they may have intermediate storage behaviour. Various genera of Rubiaceae have been listed as having species with orthodox (desiccation tolerant) seeds, including *Alseis*, *Anthocephalus*, *Asperula*, *Bertiera*, *Cephalanthus*, *Chomelia*, *Coutarea*, *Exostema*, *Galium*, *Guettarda*, *Hamelia*, *Houstonia*, *Kraussia*, *Lasianthus*, *Mitracarpus*, *Morinda*, *Nauclea*, *Neohymenopogon*, *Paederia*, *Palicourea*, *Phyllis*, *Psychotria*, *Randia*, *Rubia*, *Rudgea*, *Sherardia*, *Spermacoce*, *Stenostomum* and *Vangueria* (Hong et al., 1998; Daws et al., 2005; Athugala et al., 2016; Wu et al., 2019; Mattana et al., 2020; Wanda et al., 2020; Ley-López et al., 2023). Seeds of *Gardenia aubryi*, *G. brighamii*, *G oudiepe*, *G. remyi* and *G. taitensis* were short lived when stored dry under conventional seed bank conditions, but the kind of seed storage behaviour was not determined (Opgenorth et al., 2024).

In attempting to test the hypothesis that animal dispersal of seeds promotes species diversification of plants, Eriksson and Bremer (1991) used dispersal information for 427 genera of Rubiaceae. They concluded that no single dispersal trait was correlated with species diversification. However, they found large numbers of species for herbs with abiotically dispersed seeds, shrubs with animal-dispersed seeds and trees/shrubs with winged seeds, suggesting an association between species diversification and seed dispersibility. In relation to fruit dispersal by animals, Bremer and Eriksson (1992) used a phylogenetic tree for Rubiaceae based on variation in chloroplast DNA to evaluate the origins of fleshy fruits in the family. They concluded that fleshy fruits have evolved independently from dry fruits at least 12 times in the Rubiaceae, with most of these events occurring in the Eocene to Oligocene.

Thus, we now find many tribes with dry fruits and many with fleshy fruits in both subfamilies of Rubiaceae (Table 2). The five alliances of Dialypetalanthoideae each have some tribes with dry fruits and others with fleshy fruits. However, the Hamelieae in the Cinchoneae alliance has both dry and fleshy fruits. In the Rubioideae, three alliances have some tribes with dry fruits and others with fleshy fruits. All nine tribes in the Psychotrieeae alliance have fleshy fruits. Anthrospermeae and Knoxieae in the Spermacoceae alliance have both dry and fleshy fruits.

Embryo morphology in seeds of Rubiaceae

Martin (1946) illustrated the embryo for 27 species of Rubiaceae, and 20 of them had a spatulate (spoon-shaped) embryo and 7 a linear (cotyledons and hypocotyl-radicle with the same width) embryo. Three of the 20 species with a spatulate embryo have a spatulate underdeveloped embryo, that is the small embryo has cotyledons and hypocotyl-radicle but its full length is much less than that of the endosperm/seed. The seven species with a linear embryo have an embryo that is about the full length of the seed, or nearly so, and thus they have a linear fully developed embryo (*sensu* Baskin and Baskin, 2007). Part of our review involved an intensive literature research to expand our database on embryo morphology for the Rubiaceae to include all the kinds of embryos that occur in the family Rubiaceae (in addition to those illustrated by Martin (1946)) and to gain an understanding of embryo morphology in the two subfamilies and various tribes of Rubiaceae. Much attention was given to the drawings of embryos in early taxonomic works that included Rubiaceae (e.g. Gaertner, 1788, 1805–1807; Lamarck, 1791–1823; Endlicher, 1833–1835, 1837–1838; Richard, 1834; von Martius et al., 1840–1906; Raoul, 1846; Wight, 1846, 1850; Wendell, 1855–1857; Baillon, 1866–1895; Hooker, 1867–1871, 1876; Kotschy and Peyritsch, 1867; Beddome, 1874; Beccari, 1877–1890; Grandidier, 1890; Koorders and Valeton, 1897–1914). The nomenclature of all species in the embryo and germination databases (Supplementary Tables S1 and S2) was checked/modified using Plants of World Online.

In addition to the three kinds of embryos seen in Martin's (1946) work, that is spatulate (S), spatulate-underdeveloped (SU) and linear-full (LF), some seeds of Rubiaceae have a linear-underdeveloped (LU) embryo (Supplementary Table S1). Further, seeds of *Gleasonia*, *Henriquezia* and *Platycarpum* in Tribe Henriquezieae collected in the Guiana Highlands in northern South America have large foliose cotyledons that cover more than half of the radicle (Rogers, 1984), which fit Martin's definition of an investing (I) embryo. Thus, based on morphology, five kinds of embryos have been identified in the Rubiaceae.

Information on embryo morphology was found for 260 genera in 62 tribes of Rubiaceae (Supplementary Table S1). All 62 tribes, except Mitchelleae, which is restricted to the temperate zone, occur in the tropics. Ten tribes occur in both the tropical and temperate zones (Table 2). S, SU, LF, LU and I were the only kind of embryo found in 23, 6, 5, 1 and 1 tribe(s), respectively (Table 2). However, some tribes have more than one kind of embryo, for example Guettardeae and Dialypetalantheaae have S, SU and LF, while Spermacoceae have S, SU, LF and LU embryos. Fifty-four of the 62 tribes (87.1%) have an S and/or SU embryo, either alone or in combination with LF and/or LU embryos. LF and LU embryos are the only kind of embryo occurring in 8.1 and 1.6%, respectively, of the 62 tribes and both LF and LU together in 3.2% of the tribes.

Embryo morphology in subfamilies and tribes of Rubiaceae

For the Dialpetalathoideae as delineated by Razafimandimbison and Rydin (2024), we found information on embryo morphology for 36 tribes, and 31 of them have some species with S embryos (Table 2). Twelve tribes have some species with S embryos and other species with SU embryos. Two tribes have S, SU and LF embryos, and two others have S, SU and LU embryos. We found two tribes with only LF embryos and one with LF and LU embryos. We note that absence of a kind of embryo in a tribe may be due to lack of research and not to phylogeny.

For the Rubioideae, as delineated by Razafimandimbison and Rydin (2024), we found information on embryo morphology for 23 tribes (Table 2). With the exception of Colletoecemateae and Schradereae with only LF embryos and Gaertnereae with only LU embryos, all tribes have S and/or SU embryos. Thus, both subfamilies have tribes with various combinations of S, SU, LF and LU embryos, but only the Henriquezieae in the Dialypetalanthoideae has an I embryo.

We obtained 94 tribe-level records for embryo morphology in the Rubiaceae: S, 45; SU, 27, LF, 13, LU, 8 and I, 1 (Table 2). Except for I, which was found only in dry fruits, all kinds of embryos were found in both dry and fleshy fruits: S, 18 dry and 27 fleshy; SU, 10 dry and 17 fleshy; FL, 7 dry and 6 fleshy and LU 4 dry and 4 fleshy.

Table 2. Embryo morphology and seed dormancy in tropical/subtropical and temperate/Arctic regions of subfamilies and tribes of Rubiaceae (following Razafimandimbison and Rydin (2024)) and information on general distribution of tribes

Subfamily Alliance Tribe	General distribution	Type of fruit[a]	Tropical/ subtropical region embryo	Tropical/ subtropical regions ND, MD, MPD and PD	Temperate[b]/ Arctic region embryo	Temperate/ Arctic regions ND, MD, MPD and PD
Tribes unclassified to subfamily						
Acranthereae	Asia	F	(Spatulate)			
Coptosapelteae	Trop./subtrop. Asia	D	(Spatulate), linear-ud	MD		
Luculieae	Himalaya to southern China	D	Spatulate-ud	MPD		
Dialypetalanthoideae						
Cinchoneae alliance						
Chiococceae	Trop./subtrop. Amer.	F	Spatulate, spatulate-ud	MD, PD		
Chioneae	Trop. Amer.	F	(Spatulate)			
Cinchoneae	Trop. Amer.	D	Spatulate, spatulate-ud	ND, MPD		
Guettardeae	Trop./subtrop.	F	Spatulate, spatulate-ud, linear-full	ND, MPD, PD	Linear-full	PD
Hamelieae	Trop./subtrop. Amer.	D, F	Spatulate	ND		
Hillieae	Trop. Amer.	D	(Spatulate)			
Hymenodictyeae	Trop. Africa and Asia	D	Spatulate	ND		
Isertieae	Trop. Amer.	F	Spatulate	PD		
Naucleeae	Palaeotropics, Few species in Neotropics/ subtrop.	F	Spatulate, (spatulate-ud)	ND, PD	Spatulate	ND
Rondeletieae	Trop. Amer.	D	Linear-ud, (spatulate), (spatulate-ud)	MPD		
Strumpfieae	Trop. Amer.	F	(Spatulate)			
Dialypetalantheae alliance						
Dialypetalantheae	Trop.	D	Spatulate, (spatulate-ud), linear-full	ND, PD		
Henriquezieae	Trop. Amer.	D	(Investing)			
Posoquerieae	Trop. Amer.	F	Spatulate	PD		
Sipaneeae	Trop. Amer.	D	(Linear-full)			
Mussaendeae alliance						
Mussaendeae	Trop.	F	(Spatulate), spatulate-ud	MD, MPD		
Sabiceeae	Trop.	D	(Linear-full), (linear-ud)			
Vanguerieae alliance						
Aleisanthieae	Trop. Pacific	D	(Linear-full)			
Crossopterygeae	Trop. Africa	D	(Spatulate)			
Glionnetieae	Trop. Africa	D	?			

(*Continued*)

Table 2. (*Continued.*)

Subfamily Alliance Tribe	General distribution	Type of fruit[a]	Tropical/ subtropical region embryo	Tropical/ subtropical regions ND, MD, MPD and PD	Temperate[b]/ Arctic region embryo	Temperate/ Arctic regions ND, MD, MPD and PD
Greeneeae	Trop. Asia	D	Linear-full	ND		
Ixoreae	Trop./subtrop.	F	Spatulate	PD		
Scyphiphoreae	Trop.	F	Spatulate	ND		
Trailliaedoxeae	Trop. China	D	(Spatulate)			
Vanguerieae	Trop.	F	Spatulate, linear-full	ND, PD		
Coffeeae alliance						
Alberteae	Trop. Africa	D	Spatulate-ud	MPD		
Augusteae	Trop.	D	Spatulate	PD		
Bertiereae	Trop.	F	Spatulate	PD		
Coffeeae	Trop./subtrop.	F	(Spatulate), spatulate-ud	MD, MPD	Spatulate-ud	MPD
Cordiereae	Trop. Amer.	F	Spatulate, spatulate-ud	ND, MD, MPD, PD		
Gardenieae	Trop./subtrop.	F	Spatulate, spatulate-ud, (linear-ud)	ND, MD, MPD, PD	Spatulate	ND
Octotropideae	Trop.	F	(Spatulate), spatulate-ud	MPD		
Pavetteae	Trop.	F	Spatulate, spatulate-ud	MPD, PD		
Sherbournieae	Trop. Africa	F	Spatulate	ND, PD		
Tribes unassigned to alliances						
Airospermeae	Trop. Asia/Pacific	F	(Spatulate), (linear-ud)			
Jackieae	Trop. Asia/Pacific	D	(Spatulate)			
Retiniphylleae	Trop. Amer.	F	(Spatulate)			
Steenisieae	Trop. (Borneo)	D	?			
Rubioideae						
Urophylleae alliance						
Colletoecemateae	Trop. Africa	F	Linear-full			
Ophiorrhizeae	Trop./subtrop. Asia	D	Spatulate, (spatulate-ud)	ND, PD		
Seychelleeae	Trop.	F	(Spatulate-ud)			
Temnopterygeae	Trop. Africa	F	?			
Urophylleae	Trop.	F	Spatulate	ND, PD		
Permameae alliance						
Lasiantheae	Trop./subtrop.	F	(Spatulate-ud), linear-full	PD	Linear-full	PD
Perameae	Trop. Amer.	D	?			
Psychotrieae alliance						
Craterispermeae	Trop. Africa	F	(Spatulate-ud)			
Gaertnereae	Trop./subtrop.	F	Linear-ud	MD, MPD		
Mitchelleae	Temp.	F			Spatulate-ud	MPD

(*Continued*)

Table 2. (*Continued.*)

Subfamily Alliance Tribe	General distribution	Type of fruit[a]	Tropical/ subtropical region embryo	Tropical/ subtropical regions ND, MD, MPD and PD	Temperate[b]/ Arctic region embryo	Temperate/ Arctic regions ND, MD, MPD and PD
Morindeae	Trop./subtrop.	F	Spatulate-ud, linear-full	ND, MPD, PD		
Palicoureeae	Trop./subtrop.	F	Spatulate-ud	MD, MPD		
Prismatomerideae	Trop. Asia	F	(Spatulate-ud)			
Psychotrieae	Trop./subtrop.	F	(Spatulate), spatulate-ud, (linear-ud)	MD, MPD	Spatulate-ud	MD, MPD
Schizocoleeae	Trop. Africa	F	?			
Schradereae	Trop.	F	(Linear-full)			
Spermacoceae alliance						
Aitchisonieae	Asia	D	?			
Anthospermeae	Mostly Southern Hemisphere	D, F	Spatulate	PD	Spatulate	ND, PD
Argostemmateae	Trop./subtrop.	D	(Spatulate), (spatulate-ud)			
Cyanoneuroneae	Trop. Asia	F	?			
Danaideae	Trop. Africa, Indian Ocean Islands	D	(Spatulate), (spatulate-ud)			
Dunnieae	Subtrop. Asia	D	(Spatulate)			
Foonchewieae	Asia	D	?			
Knoxieae	Trop./subtrop.	D, F	(Spatulate), spatulate-ud	MPD		
Paederieae	Trop./subtrop.	D	Spatulate, linear-full	PD	Spatulate	PD
Putorieae	Trop./subtrop.	F	Spatulate	ND		
Rubieae	Temp., trop. mountains	D	Spatulate	ND, PD	Spatulate	ND, PD
Spermacoceae	Trop./subtrop.	D	Spatulate, spatulate-ud, linear-full, linear-ud	ND, MD, MPD, PD	Spatulate, linear-full	ND, PD
Theligoneae	Trop. to temp.	F	(Spatulate)			
Tribe unclassified to alliance						
Coussareeae	Trop. Amer.	F	Spatulate, spatulate-ud	ND, MPD, PD		

Amer., America; MD, morphological dormancy; MPD, morphophysiological dormancy; ND, non-dormant; PD, physiological dormancy; subtrop., subtropical; temp., temperate; trop., tropical; D, mature fruit is dry; F, mature fruit is fleshy; ud, underdeveloped; kind of embryo in parentheses (), have information on the embryo but not on germination; ?, no information is available.

[a] Information on type of fruit from Hooker and Hooker (1895), Motley et al. (2005), Backlund et al. (2007), Sonké et al. (2008), Kainulainen et al. (2009), Wen and Wang (2012), Ginter et al. (2015), Mabberley (2017), Takeuchi and Arifiani (2018), Razafimandimbison et al. (2020), Delprete (2022b) and Razafimandimbison and Rydin (2024).

[b] Can include the northern edge of the subtropical region.

Kinds of seed dormancy in Rubiaceae

Seed dormancy in Rubiaceae is related to embryo morphology and the time required for dormancy-break and germination. In seeds with a fully developed S or LF embryo, there is no growth of the embryo inside the mature seed prior to germination; thus freshly matured seeds are either ND or have physiological dormancy (PD). Seeds with a fully developed embryo are ND if they germinate to high percentages, often over a wide range of environmental conditions within about 4 weeks, and the range of environmental conditions does not increase after seeds are given a dormancy-breaking treatment (Baskin and Baskin, 2014; Supplementary Table S2). Seeds with a fully developed embryo have PD if they fail to germinate at any set of environmental conditions in about 4 weeks, or they only germinate over a limited range of conditions that increases after seeds receive a dormancy-breaking treatment (conditional dormancy). Seeds with PD have a physiological inhibiting mechanism in the embryo that prevents the embryo from having enough growth potential to overcome the mechanical restriction of the seed coat or other structures covering the embryo. Dormancy-breaking treatments such as cold (0–10°C) or warm (≥15°C) moist stratification, or in some species dry-afterripening, lead to an increase in growth potential of the embryo and thus dormancy-break (Baskin and Baskin, 2014). It should be noted that we found no information in the literature on germination of Henriquezieae seeds, which have an investing embryo. Based on the large size of the fully developed investing embryo, however, it is assumed that Henriquezieae seeds are either ND or have PD.

In seeds of Rubiaceae with an SU or LU embryo, growth of the small, differentiated (has organs) embryo occurs inside the seed prior to germination. Seeds with an underdeveloped embryo in which embryo growth and germination occur in about 4 weeks or less after seeds are placed on a moist substrate have morphological dormancy (MD). That is, the delay in germination (under favourable conditions) is caused by a morphological 'problem', which is overcome after the embryo grows to full size. In some seeds with an underdeveloped embryo, germination does not occur within about 4 weeks when seeds are incubated under favourable conditions; they have morphophysiological dormancy (MPD). In seeds with MPD, the breaking of MD (i.e. embryo growth) is prevented because the embryo has PD. PD is broken by warm and/or cold stratification or dry-afterripening, and depending on the species, the embryo grows after and/or during the treatment that breaks PD (Baskin and Baskin, 2014).

Seed dormancy in subfamilies of Rubiaceae

To supplement our database of information on seed dormancy/germination in the Rubiaceae that we have been accumulating since the late 1980s, extensive web searches were undertaken using various combinations of keywords, including names of the tribes of Rubiaceae, names of countries, grains, seeds, semillas, sementes, germinação and germinación. Information on seed dormancy/germination was found for 308 species of Rubiaceae, and 261 and 47 of them were from tropical/subtropical (hereafter tropical) and temperate/high latitude regions (hereafter temperate), respectively (Supplementary Table S2). If freshly matured seeds with a fully developed embryo germinated to a high percentage in about 4 weeks or less and dormancy-breaking treatments did not increase germination, the species was counted as having ND seeds. However, if seeds that germinated to a high percentage in about 4 weeks or less belonged to a genus/species with an underdeveloped embryo (and a dormancy-breaking treatment did not increase the range of conditions for germination), the species was counted as having MD. If seeds germinated to a low percentage, or not at all, and germination increased when seeds were given a dormancy-breaking treatment, they were listed as having dormant seeds. If the dormant seeds had a fully developed embryo, the species was listed as having PD. However, if the dormant seeds had an underdeveloped embryo, the species was listed as having MPD. In the case of PD, it was assumed that the seeds had non-deep PD, in which the excised embryo will grow and GA_3 promotes germination (Baskin and Baskin, 2014). However, see 'Concluding thoughts' for the possibility of deep PD in some tropical Rubiaceae.

An examination of the information in Table 2 reveals strong evidence that much research remains to be done on seed dormancy/germination of the Rubiaceae. Of the 71 tribes listed in Table 2, we found no information on embryo morphology or seed dormancy for eight of them (Aitchisonieae, Cyanoneuroneae, Foonchewiee, Glionnetieae, Perameae, Schizocoleeae, Steenisieae and Temnopterygeae). For 23 tribes, we found information on embryo morphology but not on seed dormancy. For 12 tribes (Coffeeae, Coptosapelteae, Dialypetalantheae, Gardenieae, Knoxieae, Lasiantheae, Mussaendeae, Naucleeae, Octotropideae, Ophiorrhizeae, Psychotrieae and Rondeletieae), we found information on embryo morphology, but information on seed dormancy is incomplete. For example, in Coptosapelteae, S (Pitard, 1922–1933) and LU (Stoffelen et al., 1996) embryos have been reported, but the only information for seed dormancy for a member of this tribe comes from a study by Mensbruge (1966) on seeds of *Corynanthe pachyceras*. Based on presence of a LU embryo in seeds of *Corynanthe* sp. (Stoffelen et al., 1996) and germination of *C. pachyceras* seeds to 80–90% (without treatment) in 8–20 days, we assume that seeds of this species have MD. It is likely that ND and/or PD occur in seeds of members of this tribe that have an S embryo.

In tropical regions, only MD and MPD have been reported in Coptosapelteae and Luculieae, while ND, MD, MPD and PD are found alone or in various combinations in 24 tribes of Dialypetalanthoideae and 14 tribes of Rubioideae (Table 2). In temperate regions, ND, MD, MPD and PD have been reported in 4 and 7 tribes of Dialypetalanthoideae and Rubioideae, respectively. In temperate Dialypetalanthoideae, seeds of Guettardeae have PD; Naucleeae, ND; Coffeeae, MPD and Gardenieae, ND. In temperate Ruboioideae, 3, 1, 1 and 2 tribes have ND/PD, MPD, MD/MPD and PD, respectively.

Some tribes have only ND (e.g. Greeneeae, Hamelieae and Scyphiphoreae), only PD (e.g. Bertiereae, Isertieae and Ixoreae) or both ND and PD (e.g. Naucleeae, Sherbournieae and Vanguerieae). It is expected that as more research is done on seeds of Rubiaceae the number of tribes with both MD and MPD as well as the number of tribes with both ND and PD will increase.

In tropical regions, each of the two subfamilies of Rubiaceae has ND seeds, or they have MD, MPD and PD, depending on the species (Table 2). However, in temperate regions, Dialypetalanthoideae is represented by species whose seeds are ND or have PD and MPD. In temperate regions, Rubioideae is represented by species whose seeds are ND, or they have MD, MPD and PD.

Seed dormancy profiles: biogeography and life forms

In the seed dormancy profile for Rubiaceae that includes all vegetation zones and life forms, 20.8% of the species had ND seeds, and 6.8, 22.1 and 50.3% had MD, MPD and PD, respectively (Table 3). Trees, shrubs, herbs and climbers account for 137. 98, 17 and 9 species, respectively, in tropical regions but for only 3, 19, 24 and 1 species, respectively, in temperate regions. Overall, 27.0% of the tropical tree species had ND seeds, and 8.0, 16.1 and 48.9% had MD, MPD and PD, respectively, with the most species in the rainforest. No trees with ND seeds were found for the tropical montane region, and MD was not found for tropical savanna and montane trees or MPD for tropical deciduous trees. MD and/or MPD occur in seeds of trees in the five vegetation regions, but overall MPD is more common than MD.

For tropical shrubs, 12.2% had ND seeds, and 8.3, 37.8 and 41.8% had MD, MPD and PD, respectively (Table 3). We found no shrubs in dry tropical deciduous forests with MD or PD or

Table 3. Dormancy profile for Rubiaceae in relation to biogeography and life form

Region/Life form	Total species	ND	MD	MPD	PD
Rubiaceae[a]	308	20.8%	6.8%	22.1%	50.3%
Tropical					
Trees	137	27.0	8.0	16.1	48.9
Rainforest (RF)	69	36.2	14.5	11.6	37.2
Semi-evergreen RF	40	17.5	0	12.5	70.0
Tropical deciduous	8	12.5	12.5	0	75.0
Savanna	9	33.3	11.1	33.3	22.2
Montane	11	0	0	63.6	36.4
Shrubs	98	12.2	8.3	37.8	41.8
Rainforest (RF)	34	20.6	11.8	17.6	50.0
Semi-evergreen RF	31	12.9	3.2	64.5	19.4
Tropical deciduous	2	50.0	0	50.0	0
Savanna	15	0	13.3	20.0	66.7
Montane	16	0	6.3	43.8	50.0
Herbs	17	41.2	0	11.8	47.0
Climbers	9	22.3	0	44.4	33.3
Temperate					
Trees	3	0	0	33.3	66.7
Shrubs	19	10.5	5.3	5.3	78.9
Herbs	24	16.6	0	4.2	79.2
Climbers	1	0	100	0	0

[a] Dormancy profile for 308 species of Rubiaceae, including all vegetation zones and life forms.

any savanna or montane shrubs with ND seeds. Among the tropical shrubs in general, MPD was more likely to occur than MD. In tropical herbs and climbers, some species had ND seeds, others had MPD or PD but none had MD.

Information for only a few temperate region species of Rubiaceae was found; thus, we constructed a life form dormancy profile for the whole region, with no consideration given to the vegetation zone. Some trees, shrubs and herbs in the temperate region have seeds with PD. ND seeds occur in some shrubs and herbs but have not been observed in any trees or climbers. Some trees, shrubs and herbs have seeds with MPD, but MD was found only for shrubs and climbers. It should be noted that the 'vivipary' reported for seeds of the herbs *Ophiorrhiza mungos* (Dintu et al., 2015) and *O. tomentosa* (Tan and Rao, 1981) are cases of ND orthodox seeds germinating in fruits during the rainy season and not true vivipary. That is, continuous rainfall promoted the germination of the ND seeds before they were dispersed (see Lu et al., 2022; Baskin and Baskin, 2023).

Flower sexual morphology and seed dormancy/germination

Flowers of Rubiaceae mostly are bisexual, but some species are dioecious or rarely polygamo-dioecious or monoecious (Robbrecht, 1988). Many species of Rubiaceae have heterostylous flowers, and Darwin (1877) observed that heterostyly is very common in this family. However, many Rubiaceae flowers are homostylous (e.g. Delprete, 2017). The heterostylous flowers of Rubiaceae are distylous, and Naiki (2012) reported that 109 of 563 genera of Rubiaceae are distylous. In distyly, one flower morph (pin) has a long style and short stamens, and the other morph (thrum) has a short style and long stamens (Sobrevila, 1983; Naiki, 2012). Barrett and Richards (1990) concluded that the basic characteristics of heterostyly are the same in temperate and tropical regions. They noted that woody heterostylous Rubiaceae are not represented by trees (and by only a few shrubs) in the temperate region, but many heterostylous trees and shrubs are found in tropical forests. In the tropics, the flowers may be pollinated by bees, butterflies, flies, hummingbirds and moths (e.g. Barrett and Richards, 1990; Machado and Loiola, 2000; Massinga et al., 2005; Mendonça and Anjos, 2006).

Many pollination studies have been conducted on distylous species of Rubiaceae (e.g. Ferrero et al., 2012; Watanabe et al., 2015; Ornelas et al., 2020; Furtado et al., 2021, 2022), and the results of some of them have included information on fruit/seed set but not seed germination (e.g. Sobrevila, 1983; Murray, 1990; Ree, 1997; Massinga et al., 2005; Silva et al., 2010, 2014; Hernández-Ramírez, 2012; Martén-Rodríguez et al., 2013; Raju and Radhakrishna, 2018; Xu et al., 2018). The general conclusion from these studies is that the distylous flowers promote cross-pollination in self-incompatible species. Pollen from long stamens results in fertilization of ovules of flowers with a long style, and pollen from short stamens results in fertilization of ovules of flowers with a short style.

In a study that did include seed germination, seeds of the distylous, self-incompatible *Psychotria suterella* were collected from both flower morphs from plants growing in a non-fragmented (continuous) forest, isolated forest fragments and forest fragments connected by corridors in the Atlantic Forest in Brazil (Lopes and Buzato, 2007). Seeds were planted in a greenhouse, and germination was monitored. The authors did not analyse differences in seed germination between the flower morphs because germination did not differ significantly between the three kinds of habitats. Thus, from a plant reproduction perspective, *P. suterella* showed resilience to habitat fragmentation.

Among Rubiaceae species with hermaphroditic (perfect) homostylous flowers, self-pollination can be prevented by protandry. In *Ferdinandusa speciosa*, the male phase of flowering precedes the female phase by 1 day, but the species is self-compatible (de Castro and de Oliveira, 2001). Seeds from cross-pollinated flowers had greater mass than those from self-pollinated flowers, and they germinated to 91.7 and 43.3%, respectively. Freshly matured seeds collected from plants of the annual weed *Hedyotis corymbosa* growing in open disturbed habitats in tropical, summer–dry regions of India were dormant (Raju and Krishna, 2018). Styles and stamens in flowers of this species are the same length, and the species is self-compatible and auto-selfing but weakly protandrous. Seed dormancy is broken during the dry season, and germination occurs with the onset of monsoon rains. Flowers of the shrubs *Pavetta tomentosa* (Raju and Rao, 2016a) and *Tarenna asiatica* (Raju and Rao, 2016b) growing in the Eastern Ghats Forest in India are hermaphroditic, protandrous and are both self- and cross-compatible. Freshly matured seeds of *P. tomentosa* are ND, but germination in the field does not occur until soil moisture becomes non-limiting. Seed germination of *T. asiatica* was not evaluated, but germination in the field occurred with onset of the monsoon rains.

The somewhat dioecious species *Antirhea borbonica* has polliniferous flowers and female flowers (Litrico et al., 2005). Polliniferous flowers can produce a low number of seeds, but female flowers do not produce pollen. The polliniferous flower morph has a longer corolla tube, longer stamens, shorter style and produces more pollen but fewer seeds than the female flower morph. Seeds from female and polliniferous flowers germinated to 88 and 46%, respectively, and seedling survival was 95 and 50%, respectively. Thus, the sexual morphology of Rubiaceae flowers, in particular heterostylous flowers, has received much research attention from pollination biologists. Further, seed set from various kinds of crosses has been determined, but no detailed studies have been conducted on dormancy-break and germination of the resulting seeds. Thus, the effects (if any) of the diversity of pollination strategies in the Rubiaceae on seed dormancy/germination are not known.

Dormancy-break and germination requirements

One indication of the presence of non-deep PD in seeds is that treatments resulting in the disruption of the mechanical restriction of the seed coat allow the embryo, which has low growth potential, to germinate. Treatments of seeds of Rubiaceae that may increase germination include mechanical scarification (Msanga and Kalaghe, 1993; Parreira et al., 2011; Valente et al., 2019) and acid scarification (Sadeghi et al., 2009). Further, mechanical scarification of *Oldenlandia corymbosa* seeds removed the light requirement for germination; also, GA_3 substituted for the light requirement in this species (Corbineau and Côme, 1980/81). Soaking seeds of *Rubia tinctorum* in hot water (90°C) can promote germination (Sadeghi et al., 2009); however, depending on the species, temperature and soaking time, hot water can kill the seeds (Garwood, 1986; Sadeghi et al., 2009). Soaking seeds of Rubiaceae with PD in GA_3 (Dhiman et al., 2022) or KNO_3 solutions (Valente et al., 2019) or soaking seeds with MPD in these solutions (Campos-Ruíz et al., 2016) can promote germination, presumably by increasing the growth potential of the embryo and/or weakening the seed coat (Bewley et al., 2013).

In temperate regions, PD in seeds of Rubiaceae is broken by cold stratification during winter followed by germination in spring (Farmer, 1979; Roberts, 1986; Masuda and Washitani, 1992; Hölzel and Otte, 2004), or it is broken in summer followed by germination in autumn (e.g. Brenchley and Warington, 1930; Baskin and Baskin, 1988). Also, in temperate regions, the PD part of MPD may be broken during cold stratification during winter, for example *Mitchella repens* (Barton and Crocker, 1945), allowing seeds to germinate in spring. In seasonally wet–dry tropical regions, PD in seeds of some species of Rubiaceae is broken during the dry season followed by germination at the onset of the wet season (Raju and Krishna, 2018). PD likely is broken during the dry season via afterripening, since it is known that dry-storage promotes dormancy-break and increases germination percentages of some Rubiaceae (Grijpma, 1967; Kasera and Sen, 1987; Lugo and Figueroa, n.d.).

In tropical regions that receive rain throughout the year, germination of Rubiaceae seeds with MD can begin in 5–25 days after seed dispersal, and it may be extended for up to 50–60 days, depending on the species (Table 4). Embryo growth in seeds of *Coffea arabica* incubated on a water-moistened substrate at 30°C was detected after 1 day, and as the embryo grew the puncture force required to break the enclosing endosperm decreased (da Silva et al., 2004). ABA could inhibit an increase in pressure potential of the embryo, and the authors suggested that it also controlled the second step of endosperm cap weaking that occurs prior to germination (radicle emergence).

Germination of seeds of Rubiaceae with MPD can begin in 5–8 weeks, but depending on the species, it can continue for 14–75 weeks (Table 4). In general, the *level* of MPD in seeds of Rubiaceae has not been determined. However, seeds of *Psychotria nigra* and *P. zeylandica* from the tropical montane forests in Sri Lanka have non-deep simple epicotyl MPD (Athugala et al., 2016). Warm stratification promoted radicle emergence in 53 and 100 days for *P. nigra* and *P. zeylandica*, respectively, but 50 and 80 additional days of warm stratification, respectively, were required for the shoot to emerge. In contrast, seeds of *Gaertnera walkeri*, also from the tropical montane forests of Sri Lanka, have non-deep simple epicotyl MPD but required only *c.* 10 days for radicle emergence and another ≥ 28 days for the shoot to emerge (Athugala et al., 2018).

Germination of Rubiaceae seeds with PD in tropical regions that receive rain throughout the year generally begins in 2–6 weeks after dispersal but continues for 7–43 weeks, depending on the species (Table 4). Since the species grow in regions where soil moisture generally is not limiting for germination, we assume that dormancy-break is slow and seeds germinate as soon as they become ND. The slow breaking of PD in seeds with only PD and in those with MPD is an effective way to spread the germination of seeds in a cohort over time (see Baskin et al., 2005). Another possibility for the extended germination season of some species is that the freshly matured seed cohort is a mixture of ND seeds and those with PD. For example, a seed collection of *Calycophyllum candidissimum* from Cuba consisted of 41% ND seeds, 36% physiologically dormant seeds and 23% non-viable seeds (Gutiérrez et al., 2020).

Table 4. Examples of the time required for dormancy-break and germination of Rubiaceae species in tropical/subtropical regions with no definite dry season for seeds sown under natural temperature regimes in nurseries or shade houses

Species	Time span for dormancy-break and germination	References
Morphological dormancy		
Coffea arabica	5–15 d	da Silva et al. (2004)
Diplospora malaccense	18–42 d	Ng (1992)
Genipa americana	25–60 d	Francis (1993)
Genipa americana	12–20 d	Carvalho et al. (1998)
Genipa americana	27–99 d	Sautu et al. (2006)
Oxyceros longiflorus	21–52 d	Ng (1992)
Morphophysiological dormancy		
Amaioua corymbosa	5–14 wk	
Amaracarpus nematopodus	8–25 wk	RFK code 3472
Eumachia frutescens	12–13 wk	RFK code 3169
Gynochthodes retropila	11–16 wk	RFK code 2506
Psychotria flava	10–13 wk[a]	Paz et al. (1999)
Psychotria limonensis	17–26 wk[a]	Paz et al. (1999)
Psychotria loniceroides	6–75 wk	RFK code 3177
Physiological dormancy		
Bobea sandwicensis	4–12 wk	Stratton et al. (1998)
Faramea occidentalis	13–43 wk	Sautu et al. (2006)
Gardenia brighamii	4–5 wk	Stratton et al. (1998)
Gardenia carinata	4–7 wk	Ng (1980)
Gardenia tubifera	4–39 wk	Ng (1980)
Guettarda foliacea	9–26 wk	Sautu et al. (2006)
Morinda citrifolia	5–30 wk	Ng (1980)
Nauclea maingayi	2–20 wk	Ng (1980)
Nauclea sudita	2–8 wk	Ng (1980)
Porteranda scortechinii	6–11 wk	Ng (1980)
Posoqueria latifolia	4–41 wk	Sautu et al. (2006)
Psydrax odoratus	4–24 wk	Stratton et al. (1998)

[a] Time to 50% germination.

Frequently, seeds germination studies of Rubiaceae species have been conducted under ambient temperature conditions in nurseries/shade houses (Supplementary Table S2) or in the field (Lebrón, 1979; Raich and Khoon, 1990). For tropical species that have been tested in incubators, the mean (±SE) temperature at which seeds germinated to a high percentage was 23.7 ± 0.7°C. In 21 of the studies on tropical species, seeds were tested in both light and dark: 6 species, seeds required light; 7, germinated equally in light and dark; 7, germinated to higher percentages in light than in dark and 1, germinated to a higher percentage in dark than in light (Supplementary Table S2). Seeds of the hot desert herb *Plocama pendula* germinated to a higher percentage in dark than in light (Pita, 1996). For temperate species tested in incubators, the mean temperature at which seeds germinated to a high percentage was 17.7 ± 1.1°C. In 13 of the studies on temperate species, seeds were tested in both light and dark: 1 species, seeds required light; 1, germinated equally in light and dark and 11, germinated to higher percentages in light than in dark (Supplementary Table S2).

Soil seed banks

If soil samples are collected after the seed germination season has ended in the field but before dispersal of new seeds, they are likely to contain seeds that are a part of the persistent soil seed bank. We found 60 such studies in which seeds of Rubiaceae were present (Table 5). Soil seed banks have been reported for 74 species in 42 genera and 17 tribes of Rubiaceae. Shrubs/trees, herbs and climbers accounted for 61.9, 33.3 and 4.8%, respectively, of the genera and for 45.9, 50.0 and 4.1%, respectively, of the species. In the tropical region, the plant group with the most records for seed banks was shrubs > herbs > trees > climbers, and in the temperate region, the plant group with the most records for seed banks was herbs > shrubs with only one record each for

Table 5. Seed banks for Rubiaceae

Species	Life form	Tribe	Type of vegetation	Country	Seeds m^{-2}	Reference
Aidia canthioides	S/T	Gardenieae	Seasonal rainforest	China (Trop.)	+	Zhu et al. (2006)
Aidia micrantha	S/T	Gardenieae	Rainforest	Republic of the Congo (Trop.)	1.1	Douh et al. (2018)
Aidia yunnanensis	S/T	Gardenieae	Dipterocarp rainforest	China (Trop.)	75	Tang et al. (2006)
Alseis blackiana	T	Dialypetalantheae	Rainforest	Panama (Trop.)	1–22	Dalling et al. (1997); Dalling and Denslow (1998)
Breonia chinensis	T	Naucleeae	Rainforest	Papua New Guinea (Trop.)	8	Saulei and Swaine (1988)
Breonia chinensis	T	Naucleeae	Dipterocarp rainforest	China (Trop.)	245	Tang et al. (2006)
Asperula gunnii	H	Rubieae	Alpine summit	Mt. Stirling in Victoria (Australia) (Temp.)	3.3–16.7	Venn and Morgan (2010)
Asperula gunnii	H	Rubieae	Alpine herb field	Australia (Temp.)	+	Hoyle et al. (2013)
Asperula tinctoria	H	Rubieae	Grassland	Hungary (Temp.)	3.3	Csontos et al. (1996)
Asperula tinctoria	H	Rubieae	Calcareous grassland	Estonia (Temp.)	+	Kalamees and Zobel (1997)
Bertiera bicarpellata	S	Bertieae	Recently logged rainforest	Cameroon (Trop.)	3.4	Daínou et al. (2011)
Cephalanthus occidentalis	S	Naucleeae	Riverine swamp	South Carolina (USA) (Temp.)	8	Schneider and Sharitz (1986)
Chassalia laxiflora	S	Psychotrieae	Successional rainforest	Côte d'Ivoire (Trop.)	1–15	de Rouw and van Oers (1988)
Coprosma quadrifida	S/T	Anthospermeae	*Nothofagus* forest	Tasmania (Temp.)	33.3	Howard (1973)
Cordylostigma virgatum	H	Spermacoceae	Semi-arid shrubland	South Africa (Temp.)	1–27	Mndela et al. (2019)
Corynanthe macroceras	T	Naucleeae	Rainforest	Republic of the Congo (Trop.)	2.2	Douh et al. (2018)
Dimetia capitellata	S	Spermacoceae	Rainforest	Malaysia (Trop.)	14	Putz and Appanah (1987)
Exallage auricularia	S	Spermacoceae	Dipterocarp forest	Sri Lanka (Trop.)	7	Putz and Appanah (1987)
Galianthe palustris	S	Spermacoceae	Pasture	Brazil (Trop.)	4,272	Calegari et al. (2013)
Galium album	H	Rubieae	Calcareous grassland	Estonia (Temp.)	+	Kalamees and Zobel (1997)
Galium aparine	H	Rubieae	Arable soil	United Kingdom (Temp.)	1,368	Brenchley and Warington (1930)
Galium aparine	H	Rubieae	Woodland	United Kingdom (Temp.)	+	Warr et al. (1994)
Galium aparine	H	Rubieae	Coniferous forest	Idaho (USA) (Temp.)	21	Kramer and Johnson (1987)
Galium aparine	H	Rubieae	Mediterranean old field	France (Temp.)	2	Lavorel et al. (1993)
Galium aparine	H	Rubieae	Post-volcanic succession	Mt. Tarawera in New Zealand (Temp.)	25	Clarkson et al. (2002)

(*Continued*)

Table 5. (*Continued.*)

Species	Life form	Tribe	Type of vegetation	Country	Seeds m^{-2}	Reference
Galium australe	H/S	Rubieae	Regenerating *Eucalyptus* forest	Victoria (Australia) (Temp.)	7	Wang (1997)
Galium boreale	H	Rubieae	Calcareous grassland	Estonia (Temp.)	+	Kalamees and Zobel (1997)
Galium divaricatum	H	Rubieae	Burnt heathland	Spain (Temp.)	3	Valbuena and Trabaud (2001)
Galium lucidum	H	Rubieae	Mediterranean old field	France (Temp.)	2	Lavorel et al. (1993
Galium microphyllum	H	Rubieae	*Quercus-Pinus* forest	Baja California, Sur (Mexico) (Temp.)	+	Arriaga and Mercado (2004)
Galium mollugo	H	Rubieae	Woodland	Spain (Temp.)	4	Amezaga and Onaindia (1997)
Galium palustre	H	Rubieae	Young beaver pond	Quebec (Canada) (Temp.)	+	Le Page and Keddy (1998)
Galium palustre	H	Rubieae	Baltic coastal grassland	Finland (Temp.)	237.8	Jutila (2003)
Galium parisiense	H	Rubieae	Temporary pools	France (Temp.)	+	Metzner et al. (2017)
Galium philistaeum	H	Rubieae	Coastal sand dune	Israel (Trop.)	+	Yu et al. (2008)
Galium saxatile	H/S	Rubieae	Pasture	United Kingdom (Temp.)	266	Chippindale and Milton (1934)
Galium saxatile	H/S	Rubieae	Pasture	United Kingdom (Temp.)	4,158	Milton (1936)
Galium saxatile	H/S	Rubieae	Woodland	United Kingdom (Temp.)	+	Warr et al. (1994)
Galium saxatile	H/S	Rubieae	Montane grassland	United Kingdom (Temp.)	33	Miller and Cummins (2003)
Galium simense	S	Rubieae	Dry Afromontane forest	Ethiopia (Trop.)	54.4	Birhanu et al. (2022)
Galium simense	S	Rubieae	Dry Afromontane forest	Ethiopia (Trop.)	159	Teketay and Granström (1995)
Galium trifidum	H	Rubieae	Marsh	Manitoba (Canada) (Temp.)	25	Pederson (1981)
Galium triflorum	S	Rubieae	Coniferous forest	British Columbia (Canada) (Temp.)	4	Kellman (1974a)
Galium triflorum	S	Rubieae	Coniferous forest	Idaho (USA) (Temp.)	126	Kramer and Johnson (1987)
Galium uliginosum	H	Rubieae	Baltic coastal grassland	Finland (Temp.)	825.1	Jutila (2003)
Galium verrucosum	H	Rubieae	Arable soil	England (Temp.)	309	Brenchley and Warington (1930)
Galium verum	H	Rubieae	Calcareous grassland	Estonia (Temp.)	+	Kalamees and Zobel (1997)
Galium verum	H	Rubieae	Baltic coastal grassland	Finland (Temp.)	111.9	Jutila (2003)
Hamelia patens	S/T	Cinchoneae	Dry forest	Belize (Trop.)	9	Kellman (1974b)
Hedyotis fruticosa	S/T	Spermacoceae	Dipterocarp rainforest	Sri Lanka (Trop.)	3	Singhakumara et al. (2000)
Hedyotis fruticosa	S/T	Spermacoceae			+	Ekasari et al. (2021)

(*Continued*)

Table 5. (*Continued.*)

Species	Life form	Tribe	Type of vegetation	Country	Seeds m^{-2}	Reference
			Burned site in montane	West Java (Indonesia) (Trop.)		
Hedyotis philippensis	S	Spermacoceae	Rainforest	Malaysia (Trop.)	169	Putz and Appanah (1987)
Hexasepalum teres	H	Spermacoceae	*Pinus* plantation	Brazil (Trop.)	+	Gonçalves et al. (2008)
Isertia hypoleuca	T	Isertieae	Secondary rainforest	Brazil (Trop.)	+	Silva et al. (2021)
Kohautia coccinea	H	Spermacoceae	Eroded hills	Tanzania (Trop.)	46	Lyaruu and Backéus (1999)
Manettia reclinata	S/V	Spermacoceae	Secondary tropical premontane forest	Costa Rica (Trop.)	30	Young (1985)
Manettia reclinata	S/V	Spermacoceae	Successional forest	Costa Rica (Trop.)	220	Young et al. (1987)
Mitracarpus hirtus	H	Spermacoceae	Pasture	Brazil (Trop.)	1024	Calegari et al. (2013)
Mitracarpus hirtus	H	Spermacoceae	Rainforest	Republic of Congo (Trop.)	12.2	Douh et al. (2018)
Mussaenda sanderiana	S	Mussaendeae	Seasonal rainforest	China (Trop.)	10	Cao et al. (2000)
Mycetia bracteata	S	Argostemateae	Dipterocarp rainforest	China (Trop.)	180	Tang et al. (2006)
Nauclea diderrichii	T	Naucleeae	Rainforest	Republic of the Congo (Trop.)	34.4	Douh et al. (2018)
Nertera granadensis	S	Anthospermeae	Post-volcanic succession	Mt. Tatawera in New Zealand (Temp.)	45	Clarkson et al. (2002)
Oldenlandia corymbosa	H	Spermacoceae	Eroded hills	Tanzania (Trop.)	38	Lyaruu and Backéus (1999)
Oldenlandia corymbosa	H	Spermacoceae	Disturbed alluvial forest	Brazil (Trop.)	15–309	Mesquita et al. (2014)
Oldenlandia lancifolia	H/S	Spermacoceae	Agroforestry systems	Brazil (Trop.)	59	Lacerda et al. (2016)
Oldenlandia nematocaulis	H	Spermacoceae	Eroded hills	Tanzania (Trop.)	3	Lyaruu and Backéus (1999)
Opercularia echinocephala	H	Anthospermeae	Rehabilitated bauxite mining site	Western Australia (Australia) (Temp.)	21.9	Grant and Koch (1997)
Paederia foetida	H/V	Paederieae	Old field undergoing succession	Japan (Temp.)	+	Numata et al. (1964)
Palicourea guianensis	S/T	Palicoureeae	Successional forest	Costa Rica (Trop.)	29	Young et al. (1987)
Palicourea guianensis	S/T	Palicoureeae	Rainforest	Panama (Trop.)	1.3	Dalling et al. (1997)
Palicourea guianensis	S/T	Palicoureeae	Secondary rainforest	Brazil (Trop.)	+	Silva et al. (2021)
Pentodon pentandrous	H/S	Spermacoceae	Lake sediments	Florida (USA) (Temp.)	784	Fiore and Putz (1992)
Porterandia anisophyllea	T	Gardenieae	Rainforest	Malaysia (Trop.)	32	Putz and Appanah (1987)
Richardia brasiliensis	H/S	Spermacoceae	*Pinus* plantations	Brazil (Trop.)	+	Gonçalves et al. (2008)

(*Continued*)

Table 5. (*Continued.*)

Species	Life form	Tribe	Type of vegetation	Country	Seeds m^{-2}	Reference
Richardia brasiliensis	H/S	Spermacoceae	Restored forest	Brazil (Trop.)	1–11	Moressi et al. (2014)
Richardia brasiliensis	H/S	Spermacoceae	Burned site in montane	West Java (Indonesia) (Trop.)	+	Ekasari et al. (2021)
Rudgea sessilis	S/T	Palicoureeae	Seasonal rainforest	Brazil (Trop.)	0.3	Neto et al. (2007)
Sabicea amazonensis	V	Sabiceeae	Secondary rainforest	Brazil (Trop.)	+	Silva et al. (2021)
Sabicea aspera	V	Sabiceeae	Agroforestry systems	Brazil (Trop.)	16	Lacerda et al. (2016)
Sabicea brasiliensis	S	Sabiceeae	Savanna	Brazil (Trop.)	5	Andrade and Miranda (2014)
Schizoussaenda henryi	S/T	Mussaendeae	Dipterocarp rainforest	China (Trop.)	725	Cao et al. (2000)
Schizoussaenda henryi	S/T	Mussaendeae	Seasonal rainforest	China (Trop.)	185	Tang et al. (2006)
Scleromitrion diffusum	H	Spermacoceae	Seasonal rainforest	China (Trop.)	105	Cao et al. (2000)
Scleromitrion galioides	H	Spermacoceae	Pasture	Australia (Temp.)	460	McIvor and Gardener (1991)
Sherardia arvensis	H	Rubieae	Mediterranean old field	France (Temp.)	2	Lavorel et al. (1993)
Spermacoce alata	H	Spermacoceae	Burned site in montane	West Java (Indonesia) (Trop.)	+	Ekasari et al. (2021)
Spermacoce brachystema	H	Spermacoceae	Pasture	Australia (Temp.)	100	McIvor and Gardener (1991)
Spermacoce brachystema	H	Spermacoceae	Tropical savanna	Australia (Temp.)	+	Williams et al. (2005)
Spermacoce capitata	S	Spermacoceae	Savanna	Brazil (Trop.)	19	Andrade and Miranda (2014)
Spermacoce capitata	S	Spermacoceae	Restored forest	Brazil (Trop.)	+	Neto et al. (2014)
Spermacoce latifolia	S	Spermacoceae	*Pinus* plantations	Brazil (Trop.)	+	Gonçalves et al. (2008)
Spermacoce latifolia	S	Spermacoceae	Agroforestry systems	Brazil (Trop.)	37	Lacerda et al. (2016)
Spermacoce latifolia	S	Spermacoceae	Restored forest	Brazil (Trop.)	+	Neto et al. (2014)
Spermacoce ocymoides	H/S	Spermacoceae	Arable soil	Belize (Trop.)	88	Kellman (1974b)
Spermacoce ocymoides	H/S	Spermacoceae	Secondary rainforest	Brazil (Trop.)	+	Silva et al. (2021)
Spermacoce senensis	H	Spermacoceae	Semi-arid shrubland	South Africa (Temp.)	1–14	Mndela et al. (2019)
Spermacoce tenuior	H	Spermacoceae	Successional forest	Costa Rica (Trop.)	264	Young et al. (1987)
Spermacoce verticillata	S	Spermacoceae	Tropical savanna	Venezuela (Trop.)	5.6	Pérez and Santiago (2001)
Spermacoce verticillata	S	Spermacoceae	Pasture	Brazil (Trop.)	160	Calegari et al. (2013)
Spermacoce verticillata	S	Spermacoceae	Restored forest	Brazil (Trop.)	+	Neto et al. (2014)
Spermacoce verticillata	S	Spermacoceae	Agroforestry systems	Brazil (Trop.)	1,074	Lacerda et al. (2016)

(*Continued*)

Table 5. (*Continued.*)

Species	Life form	Tribe	Type of vegetation	Country	Seeds m^{-2}	Reference
Timonius timon	S/T	Guttardeae	Rainforest	Papua New Guinea (Trop.)	+	Enright (1985)
Uncaria elliptica	V	Naucleeae	Dipterocarp rainforest	Sri Lanka (Trop.)	13–40	Singhakumara et al. (2000)
Urophyllum arboretum	S/T	Urophylleae	Rainforest	Malaysia (Trop.)	71	Putz and Appanah (1987)

+, species present but no number given for seeds, m^{-2}; H, herb; H/V, herb/vine; S, shrub; S/T, shrub/tree; S/V, shrub/vine; T, tree; V, vine/liana; temp., temperate region; trop., tropical/subtropical region.

trees and climbers. Seed banks of tribes Anthospermeae and Paederieae were found only in temperate regions; those of Naucleae, Rubieae and Spermacoceae in both temperate and tropical regions; and those of the other 12 tribes only in the tropical region.

The Spermacoceae had the highest representation in the seed bank studies with 14 genera and 25 species (8 in the genus *Spermacoce*), followed by Rubieae with 3 genera and 18 species (15 in the genus *Galium*). In both the Spermacoceae and Rubieae, there are woody and herbaceous species. The Naucleeae had five genera and five (four woody and one climbing) species, and Anthospermeae had three genera and three (two woody and one herbaceous) species with seed banks. Soil seed banks of tribes Argostemateae, Bertieae, Dialypetalantheae, Gardenieae, Guettardeae, Isertieae, Mussaendeae, Palicoureeae, Psychotrieae and Urophylleae were represented by one or two genera and species that were woody; Paederieae by one herbaceous genus and species and Sabiceae by one genus with two species of climbers and one shrub.

Although soil seed bank studies provide information on the presence of seeds of Rubiaceae in the soil, they do not tell us how old the seeds are or how long they can live in the soil. A few studies have been done for species of Rubiaceae in which seeds were buried in soil in the field and their viability monitored over a period of time. Seeds of the rare *Gardenia actinocarpa* and the common *G. ovularis* were placed in nylon-mesh bags and buried at a depth of 3–7 cm in a rainforest in northern Queensland (Australia) (Osunkoya and Swanborough, 2001). Seed viability was monitored at 3-month intervals for 12 months. The time for 50% of the seeds of *G. actinocarpa* and *G. ovularis* to become non-viable was about 2 and 3 months, respectively, and 0 and 20% of the seeds, respectively, were viable at 12 months.

Seeds of *Palicourea sessilis* (syn. *Psychotria vellosiana*) were placed in nylon-mesh bags and buried at depths of 5 and 15 cm in open and in shaded sites in cerrado vegetation in Brazil (Araújo and Cardoso, 2006). After 308 days of burial, seed viability ranged from 20 to 80%, with the highest viability for seeds in the shaded site at 5 cm. After about 100 days of burial, seeds began to germinate in the bags, probably in response to increased rainfall. In another study, seeds of *Palicourea marcgravii* and *Palicourea hoffmannseggiana* (syn. *Psychotria hoffmannseggiana*) were placed in nylon-mesh bags and buried at depths of 5 and 15 cm in open and in shaded sites in cerrado vegetation in Brazil (Araújo and Cardoso, 2007). After 308 days of burial, seed viability of *P. marcgravii* ranged from 15 to 60% with the highest viability of seeds in the open site at 15 cm, and seed viability for *P. hoffmannseggiana* ranged from 30 to 53% with the highest viability for seeds in the shaded site at 5 cm.

Fruits (natural dispersal unit) of the invasive vine *Paederia foetida* were placed in nylon-mesh bags on the soil surface and lightly covered with plant litter in forest interior, forest edge and open grassland in Hillsborough County, Florida (USA) (Liu and Pemberton, 2008). In the forest interior, forest edge and grassland, seed viability after 1 year was 38, 1.2 and 1.1%, respectively; after 2 years 3.3, 0.3 and 0%, respectively; and after 3 years 0.2, 0.1 and 0%, respectively. Seeds of *Asperula arvensis* and *Galium tricornutum* were placed in nylon-mesh bags and buried at a depth of 10 cm in southeastern France, which has a Mediterranean climate (Saatkamp et al., 2009). After 2.5 years, 0 and 6% of the *A. arvensis* and *G. tricornutum* seeds, respectively, were viable. For *A. arvensis*, seed viability decreased from 100% in early autumn to 10% the following spring, possibly due in part to *in situ* germination.

Some information about persistence of seeds on/in soil can be obtained by monitoring the germination of seeds in long-term germination phenology studies. Seeds of *Galium mollugo* and *Sherardia arvensis* sown outdoors in Wellesbourn, England, germinated in years 1, 2 and 3, with only 0.1 and 0.2% (of the sown seeds), respectively, germinating in year 3 (Roberts, 1986). We collected seeds of eight species of Rubiaceae from Kentucky-Tennessee (USA) and immediately planted them on the soil surface in a non-heated glasshouse in Lexington, Kentucky. The seeds were exposed to natural seasonal temperature cycles (Baskin et al., 2019) and simulated summer–wet/dry and winter–wet soil moisture conditions. Germination was monitored at weekly intervals until at least 1 year after the appearance of the last seedling. Seedlings were removed during each monitoring, and there was no input of new seeds during the study. Seed germination of the five winter annuals occurred only in autumn, and depending on species and year of planting, seeds germinated over a 2- to 5-year period (Table 6). Seeds of the summer annual *Hexasepalum teres* germinated only in spring. Seeds of this species planted in 1978 germinated over a 3-year period, but those planted in 1979 germinated over a 5-year period. Seeds of the two polycarpic perennials germinated only in the first year (spring) after planting in autumn. Although we do not know why some seeds of annual species were delayed for 2–5 years, the delay in germination does show that seeds remained viable and thus formed at least a short-lived persistent soil seed bank (Thompson et al., 1997).

Concluding thoughts

In the two subfamilies of Rubiaceae and in both tropical and temperate regions, we find seeds that are ND, as well as those with MD, MPD and PD. However, the diversity of life forms in

Table 6. Germination of seeds of Rubiaceae planted on soil in the non-heated greenhouse in Lexington, Kentucky (USA)

Species	Tribe	Life cycle	Year planted	Final germination (%)	Year(s) seeds germinated
Galium aparine	Rubieae	Winter annual	1971	64.0	3
Galium laevipes	Rubieae	Winter annual	1971	32.8	2
Galium parisiense	Rubieae	Winter annual	1970	59	5
Galium parisiense	Rubieae	Winter annual	1971	48.8	2
Galium virgatum	Rubieae	Winter annual	1970	36.3	4
Gallium virgatum	Rubieae	Winter annual	1971	62	4
Hexasepalum teres	Spermacoceae	Summer annual	1978	55.5	3
Hexasepalum teres	Spermacoceae	Summer annual	1979	56.0	5
Houstonia purpurea var. *calycosa*	Spermacoceae	Polycarpic perennial	1969	46.5	1
Houstonia pusilla	Spermacoceae	Winter annual	1970	34.8	3
Houstonia pusilla	Spermacoceae	Winter annual	1971	54.8	2
Stenaria nigricans	Spermacoceae	Polycarpic perennial	1969	41.8	1

temperate regions with ND, MD, MPD and PD is lower than that in the tropics, with only temperate-region shrubs having seeds with MD, MPD or PD as well as ND seeds. Herbs are the second most diverse life form of Rubiaceae in the temperate region, and they have seeds with MPD and PD seeds as well as ND seeds. Thus, the overall diversity of seed dormancy (including ND) is the same in tropical and temperate regions, but in temperate regions, ND and MD, MPD and PD are not represented by all life forms. With an increase in distance from the Equator or increase in elevation on mountains, the number of life forms and kinds of dormancy decrease. At the high latitude/elevation limits of distribution of Rubiaceae, boreal and tundra species of this family are herbs, and their seeds have PD (Supplementary Table S2).

The Rubiaceae is diverse in terms of embryo morphology (I, S, SU, LF and LU), seed dormancy (ND and MD, MPD and PD) and life forms, and this diversity is centred in tropical regions of the world. In particular, large numbers of trees and shrubs whose seeds are ND or have MD, MPD or PD grow in tropical rainforest and in semi-evergreen rainforests. It is interesting to contrast the diversity of embryo morphology and seed dormancy of Rubiaceae and Asteraceae. Although Rubiaceae has five morphological kinds of embryos and ND seeds as well as those with MD, MPD and PD, the extent of its world distribution is much less than the extensive worldwide distribution of Asteraceae with one kind of embryo (S) and either ND or PD seeds (cypselae) (Baskin and Baskin, 2023).

Both Rubiaceae and Asteraceae have species that are trees, shrubs, herbs and climbers, with trees in both families restricted to the tropics. In the Rubiaceae, species diversity is mostly attributed to trees and shrubs in the tropics, while the Asteraceae has high diversity of shrubs and herbs in tropical and temperate regions, as well as trees in the tropics. Dormant cypselae of Asteraceae have non-deep PD, and all six known *types* of non-deep PD are found among species of Asteraceae. The great diversity of Asteraceae species, in part has been attributed to the diversity of types of non-deep PD, which provide great lability for adaptation to new environments and ultimately species diversification (Baskin and Baskin, 2023).

Little research has been done to determine the level of PD (non-deep, intermediate and deep) and types of non-deep PD (1, 2, 3, 4, 5 and 6) in Rubiaceae. For temperate-zone herbaceous species of Rubiaceae that undergo dormancy-break in summer (e.g. *Galium aparine*, *Houstonia pusilla* and *Sherardia arvensis*) or winter (*Hexasepalum teres*) and germinate in the subsequent autumn and spring, respectively, it seems reasonable that the seeds have non-deep PD. However, little work has been done to investigate changes in temperature requirements for germination during dormancy-break of species of Rubiaceae. Our preliminary studies on dormancy-break in seeds of *H. teres* during cold stratification indicated that the minimum temperature at which seeds can germinate decreases, that is type 2 of non-deep PD. Further, the germination of seeds of the winter annuals *Galium parisiense* and *G. virgatum* and the summer annual *Hexasepalum teres* over a 4- to 5-year period in a non-heated greenhouse (Table 6) where seeds were exposed to seasonal temperature changes in Kentucky (USA) hints that dormancy cycling may occur in seeds of these species. Dormancy cycling is known to occur only in seeds with non-deep PD or those with non-deep simple MPD (Baskin and Baskin, 2014).

Unlike the Asteraceae with only non-deep PD, the prolonged period of incubation required for seed germination in some tropical species of Rubiaceae, for example *Faramea occidentalis* (13–43 weeks) and *Guettarda foliacea* (9–26 weeks) (Table 4), may indicate the presence of deep PD. One example of a tropical species with deep PD is *Leptecophylla tameiameiae* (Ericaceae) from Hawaii (USA). Seeds germinated over a period of 16–162 weeks, but when the study was terminated some viable seeds remained (Baskin et al., 2005). If seeds have deep PD, the excised embryo does not grow or if it grows a dwarf plant results (nanism). Also, GA_3 does not promote the germination of seeds with deep PD (Baskin and Baskin, 2014, 2022). Studies on seeds of tropical Rubiaceae that take a long time to germinate potentially would add much to our understanding of the variation in PD in tropical regions.

The diversity of embryo morphology and seed dormancy in Rubiaceae is associated with high species richness, especially trees and shrubs, in the tropics but not in temperate regions. However, various kinds of embryos and seed dormancy are found in Rubiaceae growing in temperate regions, suggesting that the low species richness of Rubiaceae in temperate regions is not due to lack of diversity of embryo morphology or seed dormancy *per se*. Since the Rubiaceae was widely distributed on earth by the Paleocene–Eocene (Graham, 2009), much tribe/genus diversification of this family occurred when the climate was warm. According to Graham (2009), the Miocene was also a period of great diversification of Rubiaceae, but by this time temperate climates with cold winters had developed in some parts of the world due to global cooling at the Eocene–Oligocene boundary (Toumoulin et al., 2022). Any new species of Rubiceae that diverged in vegetation regions with cold winters would have been cold tolerant, which was mostly herbs. Further, since PD is the most labile class of dormancy (Willis et al., 2014), it seems reasonable that newly formed species of Rubiaceae in regions with cold winters would have seeds with PD. Thus, today herbs whose seeds have PD are the only Rubiaceae found at high latitudes in boreal/tundra plant communities.

Supplementary material. To view supplementary material for this article, please visit: https://doi.org/10.1017/S0960258524000278.

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