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***Author for Correspondence:**
Carol C. Baskin,
E-mail: carol.baskin@uky.edu

Seed (true seed plus endocarp) dormancy in Anacardiaceae in relation to infrafamilial taxonomy and endocarp anatomy

Jerry M. Baskin[1] and Carol C. Baskin[1,2]*

[1]Department of Biology, University of Kentucky, Lexington, KY 40506, USA and [2]Department of Plant and Soil Sciences, University of Kentucky, Lexington, KY 40546, USA

Abstract

Information in the literature and unpublished results of the authors on *Dobinea* were used to determine the kind [class(es)] of seed (true seed + endocarp) dormancy and of non-dormancy of genera in all five tribes of Anacardiaceae, and the results were examined in relation to the taxonomic position and endocarp anatomy within the family. Reports of both seed germination and endocarp anatomy were found for 15 genera in tribe Spondiadeae, 6 in tribe Anacardieae, 30 in tribe Rhoeae, 3 in tribe Semecarpeae and 1 in tribe Dobineeae. In Spondiadeae (*Spondias*-type endocarp), Anacardieae, Semecarpeae and Dobineeae (*Anacardium*-type endocarp), seeds are either non-dormant (ND) or have physiological dormancy (PD). In Rhoeae (*Anacardium*-type Rhoeae Groups A, B, C and D endocarps), on the other hand, seeds are ND or have physical dormancy (PY), PD or PY + PD. PY/PY + PD in this tribe seems to be restricted (or nearly so) to *Rhus s.s.* and closely related genera (e.g. *Cotinus*, *Malosma* and *Toxicodendron*) with an *Anacardium*-type Rhoeae Group A endocarp. However, seeds of other genera (e.g. *Astronium* and *Schinus*) with this type of endocarp and those with Rhoeae Group B (e.g. *Pistacia*), Group C (e.g. *Pentaspadon*) and Group D (e.g. *Heeria*) endocarps are either ND or have PD. The fossil fruit record strongly suggests that present-day relationships between diaspore dormancy (or non-dormancy), endocarp structure and taxonomic position within Anacardiaceae extend back to at least the Palaeogene.

Introduction

> The family Anacardiaceae presents some of the most remarkable examples of seed protection by means of a hard woody endocarp, as well as some of the most ingenious devices to allow of the escape of the germinating embryos (Hill, 1933).

The large cashew family Anacardiaceae (Magnoliidae, Sapindales) consists of 82 genera and 950 species. It includes two subfamilies and five tribes: Anacardioideae [tribes Anacardieae (Mangiferae sensu Engler, 1892), Dobineeae, Rhoeae and Semecarpeae] and Spondioideae (tribe Spondiadeae). The family is monophyletic and sister to the Burseraceae. The Anacardiaceae consists mostly of trees, shrubs and lianas, and its geographical distribution primarily is pantropical, with some members, for example *Cotinus*, *Rhus* and *Toxicodendron*, extending into the temperate zone. It occurs on all of the continents except Antarctica. The fruit type of most members (c. 80% of genera) of the Anacardiaceae is a drupe, and its highly variable endocarp anatomy is a central issue in determining the kind of seed dormancy (or non-dormancy). The family has a fossil fruit record that extends back to the Palaeogene. Regarding germination, some members of subfamily Spondioideae have an operculum ('germination lid') in the endocarp, while this structure is absent in subfamily Anacardioideae (Engler, 1892; Hill, 1933, 1937, 1939; Mitchell and Mori, 1987; Wannan and Quinn, 1990, 1991; Gadek et al., 1996; Pell, 2004; Mitchell et al., 2006; Wannan, 2006; Pell et al., 2008, 2011; Weeks et al., 2014; APG IV, 2016; Mabberley, 2017; Wheeler and Madeira, 2017; Herrera et al., 2018).

The germination unit of most species of Anacardiaceae is the drupe (or more specifically the true seed + endocarp; hereafter seed). Furthermore, the seed coat does not contain a mechanical layer. Thus, the functional roles of the seed coat, namely embryo protection and regulation of germination, are performed by the endocarp. In a few species (e.g. *Pleiogynium*), the mesocarp also is stony and helps to protect the seed. In a few genera, the endocarp of the mature fruit is water-impermeable, and thus, the seed has physical dormancy (PY), which may be combined with physiological dormancy (PD), that is combinational dormancy (PY + PD). However, in most genera, the endocarp is water-permeable, and the seed either is non-dormant (ND) or has PD. The embryo is fully

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Table 1. Classification of endocarp structure (anatomy) in Anacardiaceae (primarily from Wannan and Quinn, 1990, except *Anacardium*-type tribe Rhoeae Group D from von Teichman, 1991, 1998; von Teichman and van Wyk, 1996)

***Spondias*-type of endocarp**. Strongly lignified, irregularly oriented sclerenchyma with valves or opercula (germination lids) that are dislodged at germination; opercula restricted to this type of endocarp. (Note that the *Spondias*-type of endocarp occurs in all genera of Tribe Spondiadeae, two genera of Rhoeae and one genus of Anacardieae.)

Tribe Spondiadeae occurs throughout this tribe.
Tribe Rhoeae, two genera (*Campnosperma* and *Pentaspadon*), endocarp similar to Spondiadeae.
Tribe Anacardieae, *Buchanania*, endocarp similar to Spondiadeae.

***Anacardium*-type of endocarp**. Discretely layered, regularly arranged; often contains palisade-like sclereids.

Tribe Rhoeae (excluding the Group C genera *Campnosperma* and *Pentaspadon*).
Group A. Four discrete layers of cells; inner three palisade-like sclereids (NI, inner layer; NM, middle layer; NO, outer layer) and outer layer crystalliferous (NC), for example *Astronium*[a], **Cotinus*, **Lithraea*, *Ozoroa*, **Rhus s.s.*, *Schinus* and **Toxicodendron.*
Group B. Two to three discrete layers of thin-walled parenchyma; perhaps derived from Group A via loss of NM and/or NO (i.e. middle layers); crystalliferous layer (NC) always present, for example *Pistacia*.
Group C. Irregularly oriented sclereids; no arrangement into four layers and no discrete layers of palisade-like sclereids.
Group D. Thin, two-layered; comprised of sclereids, for example *Heeria*, *Protorhus longifolia* and *Smodingium*.

Tribe Anacardieae (excluding *Buchanania*). Wide range of endocarp structure. In *Anacardium*, two to three discrete cell layers – NI and NM with palisade-like sclereids; sometimes with NO layer, but never with NC layer; closely comparable with Rhoeae Group A endocarp. In *Swintonia*, two to three discrete layers of non-lignified parenchyma – rather like endocarp of Rhoeae Group B. In *Mangifera*, lignified NI, one to two middle layers (N) and NC. In *Bouea*, similar to *Mangifera*, although endocarp mostly is one cell thick, that is inner epidermis (N).

Tribe Semecarpeae. A discrete layer of radially elongated, palisade-like sclereids (NI) bounding locule and one or two layers of smaller cells (NM and NO), sometimes lignified, for example *Semecarpus*.
Tribe Dobineeae. Four layers; NI and NM composed of palisade-like sclereids, NO and NC non-lignified, NC non-crystalliferous; related to Group A of Rhoeae.

Toxicodendron endocarp anatomy is from Copeland and Doyel (1940). Only those genera for which we have information on germination are included as examples of groups and subgroups. An asterisk (*) indicates a water-impermeable endocarp, that is physical dormancy and/or physical + physiological dormancy in the genus.
[a]Wannan and Quinn (1990) classified the *Astronium* endocarp as *Anacardium*-type Rhoeae Group A based on *Astronium urundeuva* fruit morphology. However, this species has been synonymized as *Myracrodruon urundeuva* (see de Lima et al., 2022). Carmello-Guerreiro and Paoli (2000) demonstrated that the pericarp structure of *Astronium graveolens* lacks the four-layered Rhoeae Group A endocarp as defined by Wannan and Quinn (1990) for *Astronium*. Carmello-Guerreiro and Paoli (2000) concluded that the two-layered endocarp of *A. graveolens* is *Anacardium*-type B of Wannan and Quinn. de Lima et al. (2022) studied the fruit morphology of seven of the eight species of *Astronium* and the two species of *Myracrodruon*, and they observed the same pattern in all *Astronium* species except one, in agreement with Carmello-Guerreiro and Paoli (2000). de Lima et al. (2022) concluded that *Anacardium*-type Rhoeae Group A endocarp was present in *Myracrodruon* but not in *Astronium*.

developed, and the endosperm is scant or absent in mature seeds. Thus, the seed cannot have morphological dormancy or morphophysiological dormancy (Hill, 1939; Corner, 1976; von Teichman, 1988b, 1991; Baskin and Baskin, 2014 and references cited therein).

There is considerable variation in endocarp anatomy within Anacardiaceae. Wannan and Quinn (1990) recognized two distinct basic types of endocarps within the family: the *Spondias*-type and the *Anacardium*-type (Table 1). The *Spondias*-type occurs throughout the tribe Spondiadeae, and the *Anacardium*-type occurs in the other four tribes of the family. However, the endocarps of *Buchanania* of tribe Anacardieae and of *Campnosperma* and *Pentaspadon* of tribe Rhoeae are similar to those of the *Spondias*-type (Wannan and Quinn, 1990). Furthermore, within the tribe Rhoeae, Wannan and Quinn (1990) defined three groups (subtypes) of endocarps (A, B and C), and von Teichman (1991, 1998) and von Teichman and van Wyk (1996) added a fourth one (i.e. Group D) (Table 1).

The primary aim of this review was to determine the relationship between kind (class, sensu Baskin and Baskin, 2021) of seed dormancy (or non-dormancy), taxonomic position and endocarp anatomy within the family Anacardiaceae. In particular, we wanted to know if PY and PY + PD are associated only with the *Anacardium*-type Rhoeae Group A endocarp, such as it is in the *Rhus s.s.* species (Li et al., 1999a,b,c,d,e). Furthermore, do all taxa with this endocarp subtype have PY?

Methods

An extensive literature search was conducted for information on seed dormancy in Anacardiaceae. In a number of cases, the type of seed (i.e. true seed + endocarp) dormancy was inferred from seed germination phenology studies and/or from what already was known about dormancy and how to break it in that particular taxon (genus, tribe). Seeds that germinated without pretreatment within about 30 d of sowing in either phenology or laboratory studies were considered to be ND, whereas those that required longer periods to germinate were judged to have either PY, PD or PY + PD (Baskin and Baskin, 2014). Seeds with PY or PY + PD were distinguished from those with PD based on treatment(s) required to break dormancy/imbibe water, such as treatment with GA_3 or warm and/or cold stratification for PD, mechanical scarification for PY and mechanical scarification plus cold stratification for PY + PD, endocarp anatomy and/or information on other species in the genus (see Baskin and Baskin, 2014, 2021). The kind (class) of seed dormancy of each species was examined in relation to its endocarp type or subtype and taxonomic position (subfamily, tribe) in the Anacardiaceae.

Results and discussion

We found information on both seed dormancy/germination and endocarp anatomy [i.e. *Anacardium*-type Rhoeae Groups A, B, C or D sensu Wannan and Quinn, 1990; von Teichman, 1991, 1998; von Teichman and van Wyk, 1996 and/or *Anacardium* (A1), *Anacardium* (A2) or *Spondias* (B) sensu Wannan and Quinn, 1991] for taxa in all five tribes of Anacardiaceae (Table 2). The 55 genera listed in Table 2 include 67.1% of the 82 genera and 742 (78.1%) of the 950 species in the family (sensu Mabberley, 2017). Seeds of the 15 genera of tribe Spondiadeae (*Spondias*-type endocarp) are ND or have PD, those of the six genera of Anacardieae (*Anacardium*-type endocarp) are ND or have PD, those of the 30 genera of Rhoeae (*Anacardium*-type Rhoeae Groups A, B, C and D) are ND or have PY, PD or PY + PD and those of the three genera in tribe Semecarpeae and the one genus in the tribe Dobineeae (*Anacardium*-type endocarp) have ND and PD and PD, respectively. Recalcitrant seeds have been documented in 16 species and 9 genera of tribes Anacardieae (*Bouea*, *Gluta* and *Mangifera*), Rhoeae (*Heeria*, *Protorhus* and *Sorindeia*) and Spondiadeae (*Lannea*, *Spondia* and *Tapirira*) (Subbiah et al., 2019).

In the five tribes of Anacardiaceae, PY and PY + PD occur only in the Rhoeae. Furthermore, within Rhoeae, PY is restricted to those taxa with Group A endocarp anatomy (Table 1). However, although seeds of *Myracrodruon*, for example, have this type of endocarp anatomy, they do not have PY; in fact, they are ND. de Melo et al. (1979) reported that fresh seeds of *M. urundeuva* germinated to 35.5% in 14 d. In another study, Rizzini (1965) reported that seeds of *M. urundeuva* germinated to 90% after 19 d when planted under a cerrado (Brazilian savanna) climate in Brazil. Lorenzi (1992) reported that seeds of *M. urundeuva* planted on sand enriched with organic matter germinated to 80% in 8–12 d, indicating that a high percentage of the seeds of the species are ND.

For seeds of three of the genera in tribe Rhoeae, namely *Actinocheita*, *Haplorhus* and *Rhodosphaera* (Table 2), information in the literature is not sufficient for us to have high confidence in assigning a dormancy class to them. Thus, we have placed a question mark beside the dormancy class. For example, Montoya Maquin (1972) suggested that the pericarp (endocarp?) of *Haplorhus peuviana* might be impermeable to water. However, no studies were done to compare water uptake in intact *versus* scarified seeds to verify (or not) the impermeability of the endocarp.

Neither seeds of species in tribe Rhoeae with Group B (*Pistacia*), Group C (*Pentospadon*) nor Group D (*Heeria* and *Smodingium*) endocarp anatomy have PY. Seeds of *Heeria*, *Pentaspadon* and *Smodingium* are ND (Table 2). However, it appears that while seeds of some species of *Pistacia* have PD, those of others are ND. For example, seeds of *Pistacia lentiscus* germinated to ≥75% without any treatment (Piotto, 1995; Garcia-Fayos and Verdú, 1998). Neither mechanical scarification, prechilling nor scarification + prechilling significantly increased germination percentages over that of the control. The only effect of these treatments was to cause a small, but significant, increase in germination rate (speed). Furthermore, Morrero (1949) reported that average time after sowing to germination for three sowings of *P. chinensis* seeds was 12 d.

Based primarily on the number of carpel lobes of female flowers and on endocarp anatomy (see Table 3), Wannan and Quinn (1991) provided a tentative taxonomic arrangement of genera within Anacardiaceae. They used these various characters for placement of genera in this family into either Group A or Group B (not to be confused with Rhoeae endocarp Group A and Rhoeae endocarp Group B sensu Wannan and Quinn, 1990), which were subdivided into two subgroups (Table 3). Wannan and Quinn's (1991) scheme uses endocarp anatomy as one of the characters to subdivide Group A into Subgroups A1 and A2, but it uses only characters of the gynoecium to subdivide Group B into Subgroups B1 and B2. Since they did not use endocarp anatomy to subdivide genera in Group B into Subgroups B1 and B2, genera in this group included in our study are indicated as 'Spondias (B)' in Table 2. With regard to endocarp anatomy, it is shown in Table 2 how the genera for which we have information on both seed dormancy/germination and endocarp anatomy fit into both of Wannan and Quinn's (1990, 1991) arrangements.

Applying Wannan and Quinn's (1991) taxonomic arrangement to the 55 genera in Table 2, the following can be seen. (1) Four of the six genera in Anacardieae are in Subgroup A1, one (*Anacardium*) in *Anacardium* Subgroup A2 and one (*Buchanania*) in *Spondias* Group B. (2) With only one exception (*Anacardium*), all genera in Subgroup A2 are in tribe Rhoeae. (3) All genera in Group B belong to Spondiadeae, except *Buchanania* (Anacardieae), *Campnosperma* (Rhoeae) and *Pentaspadon* (Rhoeae). (4) All genera with PY or PY + PD are in Subgroup A2. However, this Subgroup also includes genera with ND seeds, PD seeds and both ND and PD seeds.

The fossil fruit record shows that species of Anacardiaceae with PY (*Rhus s.s.*) and ND/PD (*Anacardium* and the extinct genus *Pentoperculum*, Spondiadeae) extend at least as far back as the Eocene (Manchester, 1994; Manchester et al., 2007; Herrera et al., 2018 and references cited for fossil endocarps of subfamily Spondioideae; Flynn et al., 2019; Manchester and Judd, 2022). Baskin et al. (2000) suggested that PY + PD may have originated in the Oligocene, in conjunction with climatic cooling. According to Wannan and Quinn (1990), 'The occurrence of the *Spondias*-type of endocarp in a genus [*Conarium*, Burseraceae] of the sister group [of Anacardiaceae] suggests that this type of endocarp is plesiomorphic and that the *Anacardium*-type is derived.' In this case, a water-impermeable endocarp and thus PY and PY + PD are derived in subfamily Anacardioideae. Furthermore, the diaspores of Burseraceae do not have PY or PY + PD, and the embryo is fully developed; they are either ND or have PD (e.g. Ng, 1991; Sautu et al., 2007; Baskin and Baskin, 2014; Rodríguez-Arévalo et al., 2017). However, PY/PY + PD does occur in two other families of Sapindales (sensu APG IV, 2016), namely Biebersteinaceae (Boesewinkel, 1997; Koutsovoulou et al., 2005) and Sapindaceae (Baskin et al., 2004; Turner et al., 2006, 2009; Cook et al., 2008). In Anacardiaceae and Biebersteinaceae, the water-impermeable layer in diaspores with PY/PY + PD is the endocarp of the fruit, but in the Sapindaceae, the water-impermeable layer is in the seed coat.

Concluding remarks

Seeds with PY or PY + PD in Anacardiaceae have evolved only in tribe Rhoeae and only in genera with the *Anacardium*-type Rhoeae Group A endocarp anatomy. However, neither PY nor PY + PD is present in seeds of all genera that have this specialized anatomical endocarp type. Two distinct morphoanatomical features of the seed/fruit (endocarp) of diaspores with PY are the water-impermeable palisade (macrosclereid) layer(s) with a *linea lucida* (light line) and a water gap (or water gap complex) that opens (permanently) in response to an environmental signal, thereby serving as the initial predetermined pathway for the entrance of water into the seed (e.g. Hamly, 1932; Christiansen

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Table 2. Types of endocarp and kinds of seed dormancy (or non-dormancy) in Anacardiaceae

Tribe/genus	Endocarp type	Kind of dormancy (or non-dormancy)	References
Spondiadeae			
Antrocaryon	*Spondias* (B)	ND, PD	Mensbruge (1966), Miquel (1987) and Nchanji and Plumptre (2003)
Choerospondias (=*Spondias axillaris*)	*Spondias* (B)	ND, PD	Blakesley et al. (2002), Pakkad et al. (2003), Kitamura et al. (2007), Lu et al. (2017) and Liu et al. (2021)
Cyrtocarpa	*Spondias* (B)	PD	Rodríguez-Arévalo et al. (2017)
Dracontomelon	*Spondias* (B)	ND, PD	Ng (1973, 1991), Kanzaki et al. (1997), Ancrenaz et al. (2006), Ellis et al. (2007) and Liu et al. (2021)
Haematostaphis	*Spondias* (B)	ND, PD	Agbogan et al. (2014)
Harpephyllum	*Spondias* (B)	ND	Dlamini (2004)
Koordersiodendron	*Spondias* (B)	ND, PD	Lapitan (1988), Ancrenaz et al. (2006) and Gentallan et al. (2018)
Lannea	*Spondias* (B)	ND, PD	Troup (1921), Mensbruge (1966), von Teichman (1987, 1988a), Beniwal and Singh (1989), Msanga (1998), Pritchard et al. (2004), Nichols (2005), Neya et al. (2008) and Agbogan et al. (2014)
Operculicarya	*Spondias* (B)	ND, PD	Seeds.com and Sunshine-seeds b
Pleiogynium	*Spondias* (B)	ND, PD	Ralph (1997), Sunshine-seeds c and Australian Tropical Rainforest Plants 392
Poupartia	*Spondias* (B)	ND, PD	Carvalho et al. (1998)
Pseudospondias	*Spondias* (B)	ND, PD	Mensbruge (1966), Takasaki (1983), Miquel (1987) and Wrangham et al. (1994)
Sclerocarya	*Spondias* (B)	PD	von Teichman et al. (1986), Lewis (1987), Holtzhausen et al. (1990), Msanga (1998), Jøker and Erdey (2003), Gamémé et al. (2004), Pritchard et al. (2004), Moyo et al. (2009), Dlamini (2010), Agbogan et al. (2014) and Hamidou et al. (2014)
Spondias	*Spondias* (B)	ND, PD	Troup (1921), Marshall (1939), dos Reis et al. (1980), Garwood (1983), Beniwal and Singh (1989), Ng (1991), Francis (1992), Mandujano et al. (1994), Knowles and Parrotta (1995), Murali (1997), Carvalho et al. (1998), Azevedo et al. (2004), Sautu et al. (2007), Dey et al. (2016), Oboho and Nwaihu (2016), Sánchez et al. (2019) and Sautu (pers. comm.)
Tapirira	*Spondias* (B)	ND, PD	von Teichman (1990), Lorenzi (1992), Wendt and Mitchell (1995), Farji-Brenner and Silva (1996), Sautu et al. (1999, 2007), Cesarino et al. (2007), Pereira et al. (2012) and Sautu (pers. Comm.)
Anacardieae			
Anacardium	*Anacardium* (A2)	ND, PD	Madhava Rao et al. (1957), Ibikunle and Komolafe (1973), Saplaco and Revilla (1973), Alencar and Megalhaes (1979), Sabbaiah (1982/1983), Garwood (1983), Beniwal and Singh (1989), Prasad and Kandya (1992), Carvalho et al. (2005), Sautu et al. (2007) and Oboho and Nwaihu (2016)
Bouea	*Anacardium* (A1)	ND	Troup (1921) and Ng (1978, 1991)
Buchanania	similar to *Spondias* (B)	ND, PD	Troup (1921), Agrawal and Prakash (1978), Ng (1991), Prasad and Kandya (1992), Ashwath et al. (1994) Murali (1997), Ralph (1997), Naithani et al. (2004), Nandeshwar et al. (2005) and Deshpande and Yadav (2020)
Gluta (including *Melanorrhoea*)	*Anacardium* (A1)	ND, PD	Troup (1921), Holmes (1954), Raich and Khoon (1990), Ng (1991), Elliott et al. (1997), Jose and Pandurangan (2003, 2005) and Ellis et al. (2007)
Mangifera	*Anacardium* (A1)	ND	Troup (1921), Sharma and Rajeswaran (1970), Corbineau et al. (1986), von Teichman et al. (1988), Ng (1991), Prasad and Kandya (1992), Murali (1997), Tang et al. (2008) and Samarasinghe et al. (2022)
Swintonia	*Anacardium* (A1)	ND, PD	Ng (1991)
Rhoeae			
Actinocheita	*Anacardium* (A2)	PY?	Rodríguez-Arévalo et al. (2017)
Amphipterygium	*Anacardium* (A2)	ND	Rodríguez-Arévalo et al. (2017)

(*Continued*)

Table 2. (*Continued.*)

Tribe/genus	Endocarp type	Kind of dormancy (or non-dormancy)	References
Astronium	Rhoeae Group A, [Rhoeae Group B][a] *Anacardium* (A2)	ND, PD	Rizzini (1965), de Melo et al. (1979), Marín and Flores (2002), Salomão (2002), Braga et al. (2014), Daibes et al. (2019) and Colado et al. (2020)
Blepharocarya	*Anacardium* (A2)	ND	Goulding (2001) and Australian Tropical Rainforest Plants 219
Campnosperma	Rhoeae Group C, similar to *Spondias* (B)	ND	Tarszisz et al. (2018)
Cotinus	Rhoeae Group A, *Anacardium* (A2)	PY + PD	Heit (1967, 1968), Nokes (1986), Olmez et al. (2007, 2008, 2009), Pijut (2008), Guner and Tilki (2009) and Pipinis et al. (2014, 2017)
Euroshinus	Rhoeae Group A, *Anacardium* (A2)	ND	Australian Tropical Rainforest Plants 102
Haplorhus	*Anacardium* (A2)	PY?	Montoya Maquin (1972)
Heeria	Rhoeae Group D, *Anacardium*, (A2)	ND	von Teichman and van Wyk (1996) and Deng et al. (2010)
Lithraea	Rhoeae Group A, *Anacardium* (A2)	PY	Zegers and Lechuga (1978), Lorenzi (1992), Pienaar and von Teichman (1998), Carmello-Guerreiro and Paoli (2005), Oliveira and Mariath (2015a), Gallará et al. (2017, 2021) and Gallará (pers. comm.)
Loxopterygium	*Anacardium* (A2)	ND	Agrawal (1996) and Millones-Yamunaqué et al. (2021)
Malosma	Rhoeae Group A, *Anacardium* (A2)	PY	Wright (1931), Keeley (1991) and Culshaw et al. (2002)
Mauria	Rhoeae Group B, *Anacardium* (A2)	ND, PD	Rojas-Rodríguez and Torres-Córdoba (2015)
Metopium	*Anacardium* (A2)	ND	McLaren and McDonald (2003)
Mosquitoxylum	*Anacardium* (A2)	ND, PD	Sunshine-seeds a
Myracrodruon	Rhoeae Group A, *Anacardium* (A2)	ND	Pacheco et al. (2006), Nunes et al. (2008), Vieira et al. (2008), Virgens et al. (2012), Oliveira et al. (2014a,b, 2019) and Dantas et al. (2020)
Ozoroa	Rhoeae Group A, *Anacardium* (A2)	ND	Prota4U
Parishia	Rhoeae Group B, *Anacardium* (A2)	ND, PD	Sharma and Rajeswaran (1970) and Raich and Khoon (1990)
Pentaspadon	Rhoeae Group C, *Spondias* (B)	ND	Wyatt-Smith (1964) and Ng (1980, 1991)
Pistacia	Rhoeae Group B, *Anacardium* (A2)	ND, PD	Joley and Opitz (1971), Shafik and Kettanch (1971/72), Dahab et al. (1975), Pair and Khatamian (1982), Izhaki and Safriel (1990), Piotto (1995), Garcia-Fayos and Verdú (1998), Mederos Molina and Trujillo (1999), Chaabouni and Gouta (2002), Tsakaldimi and Ganatsas (2002) and Guo et al. (2022)
Rhodosphaera	*Anacardium* (A2)	PD?	Ralph (1997)
Rhus s.s.	Rhoeae Group A, *Anacardium* (A2)	PY, PY + PD	Stone and Juhren (1951), Heit (1970), Young (1972), Atwater (1980), Farmer et al. (1982), Weber et al. (1982), Rasmussen and Wright (1988), Washitani (1988), Keeley (1991), Young and Young (1992), Doussi and Thanos (1994), Huang and Qiu (1994), Wilkinson et al. (1996), Li et al. (1999a,b,c,d,e), Ne'eman et al. (1999), Olmez et al. (2007), Rowe and Blazich (2008), Zuloaga-Aguilar et al. (2010, 2011), Bolin et al. (2011), Wang et al. (2012), Tilki and Bayraktar (2013), Lan et al. (2018) and Pullman et al. (2021)
Schinopsis	Rhoeae Group A, *Anacardium* (A2)	ND, PD	Lorenzi (1992), Oliveira and Oliveira (2008), González and Vesprini (2010), Oliveira et al. (2014a) and Santos et al. (2014)
Schinus	Rhoeae Group A, *Anacardium* (A2)	ND, PD	Zegers and Lechuga (1978), Panetta and McKee (1997), Nilsen and Muller (1980), Mytinger and Williamson (1987), Muñoz and Fuentes (1989), Anderson (2002), Carmello-Guerreiro and Paoli (2002), Demelash et al. (2003), Mandon-Dalger et al. (2004), Tassin et al. (2007), Funes et al. (2009), Oliveira and Mariath (2015b), Pereira et al. (2016) and Oliveira et al. (2018)

(*Continued*)

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Table 2. (*Continued.*)

Tribe/genus	Endocarp type	Kind of dormancy (or non-dormancy)	References
Searsia (= *Rhus s.l.* but not *Rhus s.s.*)	Rhoeae Group A, *Anacardium* (A2)	ND, PD	von Teichman and Robbertse (1986), von Teichman (1989), von Teichman and van Wyk (1991), Tietema et al. (1992), Weirsbye and Witkowski (2002), Refka et al. (2013), PZA.SANBI a, PZA.SANBI b and PZA.SANBI c
Smodingium	Rhoeae Group D, *Anacardium* (A2)	ND	von Teichman (1998)
Sorindeia	*Anacardium* (A2)	ND, PD	Msanga (1998) and Msanga and Berjak (2004)
Thyrsodium	*Anacardium* (A2)	ND, PD	Silva et al. (2021)
Toxicodendron	Rhoeae Group A, *Anacardium* (A2)	PY, PY + PD	Copeland and Doyel (1940), Xu and Xu (1987), Keeley (1991), Penner et al. (1999), Evans (2001), Kujawski (2001), Schiff et al. (2004), Osada (2005), Baskin and Baskin (2014) and Lan et al. (2018)
Trichoscypha	*Anacardium* (A2)	ND, PD	Mensbruge (1966), Miquel (1987) and Tsobeng et al. (2020)
Semecarpeae			
Drimycarpus	*Anacardium* (A1)	ND, PD	Ng (1991) and Prasad and Kandya (1992)
Holigarna	*Anacardium* (A1)	ND, PD	Deshpande and Yadav (2020)
Semecarpus	*Anacardium* (A1)	ND, PD	Holmes (1954), Airi et al. (1998), Panda and Hazra (2009), Khan (2015), Waman et al. (2018), Rathiesh et al. (2019) and Samarasinghe et al. (2022)
Dobineeae			
Dobinea	*Anacardium* (A2), Rhoeae Group A – like	PD	Baskin and Baskin, unpublished data

Endocarp types *Spondias* (B), *Anacardium* (A1) and *Anacardium* (A2) are from Wannan and Quinn (1991), Rhoeae Group D from von Teichman (1991, 1998), von Teichman and van Wyk (1996) and all others from Wannan and Quinn (1990). ND, non-dormancy; PD, physiological dormancy; PY, physical dormancy; PY + PD, combinational dormancy. Regarding ND *versus* PD, some species have a mixture of ND and PD, and others are wholly or primarily ND or PD.
[a]See footnote to Table 1.

Table 3. Endocarp structure included (along with characters of gynoecium, see text) in taxonomic arrangement of Anacardiaceae into two groups (from Wannan and Quinn, 1991; Wannan, 2006)

Group A. Subfamily Anacardioideae (without *Buchanania*, *Campnosperma* and *Pentaspadon*). Endocarp composed of discrete and regularly arranged layers of cells.
Subgroup A1. Endocarp with reduced number of layers (less than four) – *Bouea*, *Drimycarpus*, *Gluta*, *Holigarna*, *Mangifera*, *Semecarpus* and *Swintonia*. **Subgroup A2**. Endocarp usually with four distinct layers, mostly sclerenchymatous. *?*Actinocheita*, *Amphipterygium*, *Anacardium*, *Astronium*[a], *Blepharocarya*, **Cotinus*, *Dobinea*, *Euroshinus*, *Heeria*, **Lithraea*, *Loxopterygium*, *Mauria*, *Metopium*, *Mosquitoxylum*, *Ozoroa*, *Parishia*, *Pistacia*, **Rhus s.s.*, *Schinopsis*, *Schinus*, *Smodingium*, *Sorindeia*, *Thyrsodium* and *Trichoscypha*.
Group B. Subfamily Spondioideae (Spondiadeae plus *Buchanania*, *Campnosperma* and *Pentaspadon*). Thick endocarp usually composed of heavily lignified and irregularly oriented sclereids, except for the discrete cell layer bordering the locule. Subdivided into two groups based only on characters of gynoecium – not on endocarp, that is endocarp not used to subdivide Group B into Subgroups B1 and B2, which are not shown here.
Antrocaryon, *Buchanania*, *Campnosperma*, *Chaerospondias*, *Dracontomelon*, *Haematostaphis*, *Hapephyllum*, *Koordersiodendron*, *Lannea*, *Operculicarya*, *Pentaspadon*, *Pleiogynium*, *Poupartia*, *Pseudospondia*, *Sclerocarya*, *Spondias and Tapirira*.

Only those genera for which we have information on germination are included as examples of groups and subgroups. An asterisk (*) indicates physical dormancy and/or physical + physiological dormancy in the genus.
[a]See footnote to Table 1.

and Moore, 1959; Egley and Paul, 1981; Manning and Van Staden, 1987; Gama-Arachchige et al., 2013; Baskin and Baskin, 2014; Burrows et al., 2018; Geneve et al., 2018). In the case of diaspores, such as those of the anacardiaceous genera *Lithraea* and *Rhus s.s.* with PY, the endocarp is composed of four layers of cells; three of these are palisade macrosclereids, only one of which (osteosclereid layer) has a light line. Thus, it seems that a water-impermeable macrosclereid palisade layer with a *linea lucida* and a water gap together constitute the 'PY syndrome' in diaspores of angiosperms with a water-impermeable seed/fruit coat. In this case, the presence/absence of these morphoanatomical features can be used to determine which genera with *Anacardium*-type Rhoeae Group A endocarp have PY (or PY + PD) and which do not. A water gap ('carpellary micropyle') in

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Anacardiaceae has been identified/characterized only in *Rhus s.s.* species (Li et al., 1999b), which have an *Anacardium*-type Rhoeae Group A endocarp and PY or PY + PD (Table 2). Overall, then, a detailed anatomical comparison of water-permeable and water-impermeable *Anacardium*-type Rhoeae Group A endocarps should provide insight on why the diaspores of some genera in tribe Rhoeae have PY or PY + PD and others are ND or have PD.

With regard to determining if a seed or other diaspore is water-permeable or impermeable, it is important to keep in mind that impermeability (i.e. PY) develops either during maturation drying on the mother plant or even during post-dispersal drying (Baskin and Baskin, 2014; Jaganathan, 2016, 2022; Thusithana et al., 2021). Seeds or fruits with PY become impermeable to water only when the moisture content (MC) of the diaspore falls below a species-specific MC threshold (see Table 6.2 in Baskin and Baskin, 2014); otherwise, the diaspore will remain water-permeable. Gallará et al. (2021) showed that the drupes of *Lithraea molleoides* (Anacardiaceae) needed post-dispersal drying for the induction of PY. However, in fact, the diaspore MC at which PY is induced also can vary even between populations of the same taxon growing under different environmental conditions (Thusithana et al., 2021). And furthermore, the development of PY does not occur at the same time for all seeds in the same days-after-pollination cohort and thus not at the same MC [see discussion in Qu et al. (2010) and references cited therein]. Therefore, it is essential for the MC of diaspores be considered in addition to morphoanatomical traits (see above) in assigning PY or PY + PD to diaspores. In sum, then, the presence of the PY syndrome is an indicator of the potential of a species to develop PY, if, and only if, they reach the threshold MC during maturation or post-dispersal drying.

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