Seed Science Research (2012) **22**, 37–44
doi:10.1017/S0960258511000286

Evolution of physiological dormancy multiple times in Melastomataceae from Neotropical montane vegetation

Fernando A.O. Silveira[1,2]*, Rafaella C. Ribeiro[1], Denise M.T. Oliveira[1], G. Wilson Fernandes[2] and José P. Lemos-Filho[1]

[1]Departamento de Botânica/ICB/Universidade Federal de Minas Gerais, CP 486, 31270-901, Belo Horizonte, Minas Gerais, Brazil; [2]Ecologia Evolutiva and Biodiversidade/DBG, ICB/Universidade Federal de Minas Gerais, CP 486, 31270-901, Belo Horizonte, Minas Gerais, Brazil

(Received 7 July 2011; accepted after revision 11 September 2011; first published online 18 October 2011)

Abstract

We investigated seed dormancy among species of Melastomataceae from Neotropical montane vegetation of Brazil. Four out of 50 studied species had dormant seeds: *Miconia corallina* (Miconieae), *Tibouchina cardinalis* (Melastomeae), *Comolia sertularia* (Melastomeae) and *Chaetostoma armatum* (Microlicieae). For these four species, germinability of seeds collected in different years was always $<10\%$ and the percentages of embryoless seeds and non-viable embryos were both insufficient to explain low or null germinability. This is the first unequivocal report of seed dormancy in tropical Melastomataceae. The production of seeds with permeable seed coats and fully developed, differentiated embryos indicates the occurrence of physiological dormancy. The reconstructed phylogenetic tree of the 50 species suggests that physiological dormancy evolved multiple times during the evolutionary history of Melastomataceae in this vegetation. Physiological dormancy evolved in species and populations associated with xeric microhabitats, where seeds are dispersed in unfavourable conditions for establishment. Therefore, drought-induced mortality may have been a strong selective pressure favouring the evolution of physiological dormancy in Melastomataceae. We argue that dormancy may have been independently selected in other lineages of Cerrado plants colonizing xeric microhabitats and dispersing seeds at the end of the rainy season. The contributions of our data to the understanding of seed dormancy in tropical montane vegetation are discussed.

Keywords: *cerrado*, convergent evolution, drought-induced mortality, Espinhaço Range, rupestrian fields, seasonality

Introduction

The seed habit has contributed decisively to the evolutionary success of gymnosperms and angiosperms. Seeds provided plants with large ecological and evolutionary advantages, including extended survival periods after dispersal, increased resistance to adverse environmental conditions, increased dispersal distance and, subsequently, increased gene flow (Linkies *et al.*, 2010). Another remarkable event in the life history of seed plants was the evolution of dormancy. Among the numerous definitions of dormancy (Harper, 1977; Baskin and Baskin, 2004; Finch-Savage and Leubner-Metzger, 2006; Finkelstein *et al.*, 2008; Linkies *et al.*, 2010), a dormant seed can be defined as one that does not have the capacity to germinate in a specified period of time under any combination of normal physical environmental factors that otherwise are favourable for its germination (Baskin and Baskin, 2004). Because germination is an irreversible process, selection should favour strategies that prevent seeds from germinating under unfavourable conditions for seedling establishment (Jurado and Moles, 2002).

Here we report the occurrence of dormancy in Melastomataceae from Neotropical montane vegetation (rupestrian fields) and reconstruct a phylogenetic tree to obtain a better understanding of the evolutionary history of seed dormancy in this family. The rupestrian fields belong to the *cerrado* biome, which is the most species-rich savanna in the world, with more than 12,000 plant species (Mendonça *et al.*, 2008). The climate is seasonal with dry winters from April to September and rainy summers (Oliveira-Filho

---

*Correspondence
Email: faosilveira@gmail.com

and Ratter, 2002), and the typical landscape of the *cerrado* consists of a complex mosaic of savanna physiognomies on the well-drained interfluves with riparian forests along the watercourses (Ratter *et al.*, 1997).

Melastomataceae is the fourth most speciose family in the *cerrado* with 521 taxa (Mendonça *et al.*, 2008). This pantropical family is comprised of shrubs, woody climbers, herbs, epiphytes and trees that colonize montane to lowland forests, savannas and disturbed vegetation (Clausing and Renner, 2001). The family has about 5000 species arranged into two subfamilies and nine tribes and is ranked as the eighth largest plant family (Renner, 2004; Angiosperm Phylogeny Website, 2011).

Despite its higher diversity in the Neotropics (Renner *et al.*, 2001), reports of seed dormancy in melastomes are available only for the temperate herb *Rhexia mariana* (Rhexieae). Physiological dormancy (PD) evolved in this species as an adaptation to the climatic conditions in temperate eastern North America (Baskin *et al.*, 1999). Neotropical melastomes evolved different life-history strategies and colonized a broad diversity of habitats (Renner *et al.*, 2001), and thus we predict that dormancy may have evolved in other lineages of the family, particularly in seasonal habitats (Salazar *et al.*, 2011). Understanding the evolution of seed dormancy in melastomes is important not only to obtain insight into the reproductive ecology of tropical plants, but also because several melastomes (such as *Miconia calvescens* and *Clidemia hirta*) have become devastatingly invasive species (Meyer and Florence, 1996; Medeiros *et al.*, 1997).

In this study, we have: (1) screened for dormant seeds among 50 Melastomataceae species from Neotropical montane vegetation in Brazil; (2) determined the class of seed dormancy (*sensu* Baskin and Baskin, 2004) in the dormant species; (3) examined the processes driving the evolution of seed dormancy; and (4) discussed the phylogenetic and biogeographical implications of our findings for the general understanding of seed dormancy in montane vegetations.

Materials and methods

Study site and species

This study was conducted in four sites in south-eastern Brazil. Plant material was collected in a particular vegetation of *cerrado* known as rupestrian fields (rocky outcrop montane vegetation) in Minas Gerais, south-eastern Brazil. The rupestrian fields occur in quartzite-derived or ironstone soils above 900 m above sea level and harbour high levels of plant biodiversity and endemism (Alves and Kolbek, 2010). In this vegetation, plant communities are established on shallow, acidic, nutrient-poor and excessively drained soils (Giulietti *et al.*, 1997; Jacobi *et al.*, 2007), where plants often experience strong winds, high irradiance exposure, frequent fires, high daily thermal amplitudes and water shortage during the dry season (Giulietti *et al.*, 1997; Madeira and Fernandes, 1999). Local drainage systems dictated by topography diversify this environment by creating relatively humid (mesic) or arid (xeric) sites, often separated from each other by a few centimetres (Alves and Kolbek, 2010). Because of increasing human pressures (Giulietti *et al.*, 1997; Jacobi *et al.*, 2007), several native species of this vegetation are under the threat of extinction.

Seeds from 48 species were collected at Serra do Cipó (19°17′S, 43°35′W), located at the southern portion of the Espinhaço Range. Seeds of *Lithobium cordatum* and *Merianthera sipolisii* were collected in the Diamantina plateau (18°07′S and 44°20′W). Seeds of *Comolia sertularia* also were collected at Serra do Cabral (17°03′–18°13′S and 44°05′–44°52′W) and those of *Miconia corallina* also at the Parque Estadual do Ibitipoca (PEI) (21°40′–21°44′S and 43°52′–43°55′W). The dominant vegetation in all studied sites consists of rupestrian fields, but sites differ in climate and in surrounding vegetation. Serra do Cipó and Diamantina are located in a transition zone between the Cerrado and the Atlantic Forest. However, their western side (where seeds of this study were collected) and the Serra do Cabral are both associated with the Brazilian Cerrado, whereas the dense rupestrian fields of PEI are enclosed by the more humid semideciduous Atlantic Forest (Chiavegatto, 2005; Alves and Kolbek, 2010). All sites are under the influence of seasonal climates with a 4–6-month dry and cold season, but relatively higher annual rainfall occurs at PEI compared to the other sites (Madeira and Fernandes, 1999; Chiavegatto, 2005; Hatschbach *et al.*, 2006).

We investigated seed dormancy in 50 species of Melastomataceae belonging to 17 genera and four tribes (see supplementary Table S1, available online only at http://journals.cambridge.org). These species represent nearly 10% of Melastomataceae from the *cerrado*. Species selection was oriented towards maximizing life-history strategies, phylogenetic diversity and microhabitat occupancy. Germination experiments were conducted over a wide range of temperature and light conditions for these species (data not shown) and focus was given to four species showing germinability of fresh seeds $<10\%$. Our species selection was phylogenetically oriented and included species in the main lineages (Tribes) within the family. Figure 1 shows the reconstructed phylogeny of the 50 species (see supplemental material, Phylogenetic reconstruction method, available online only at http://journals.cambridge.org).

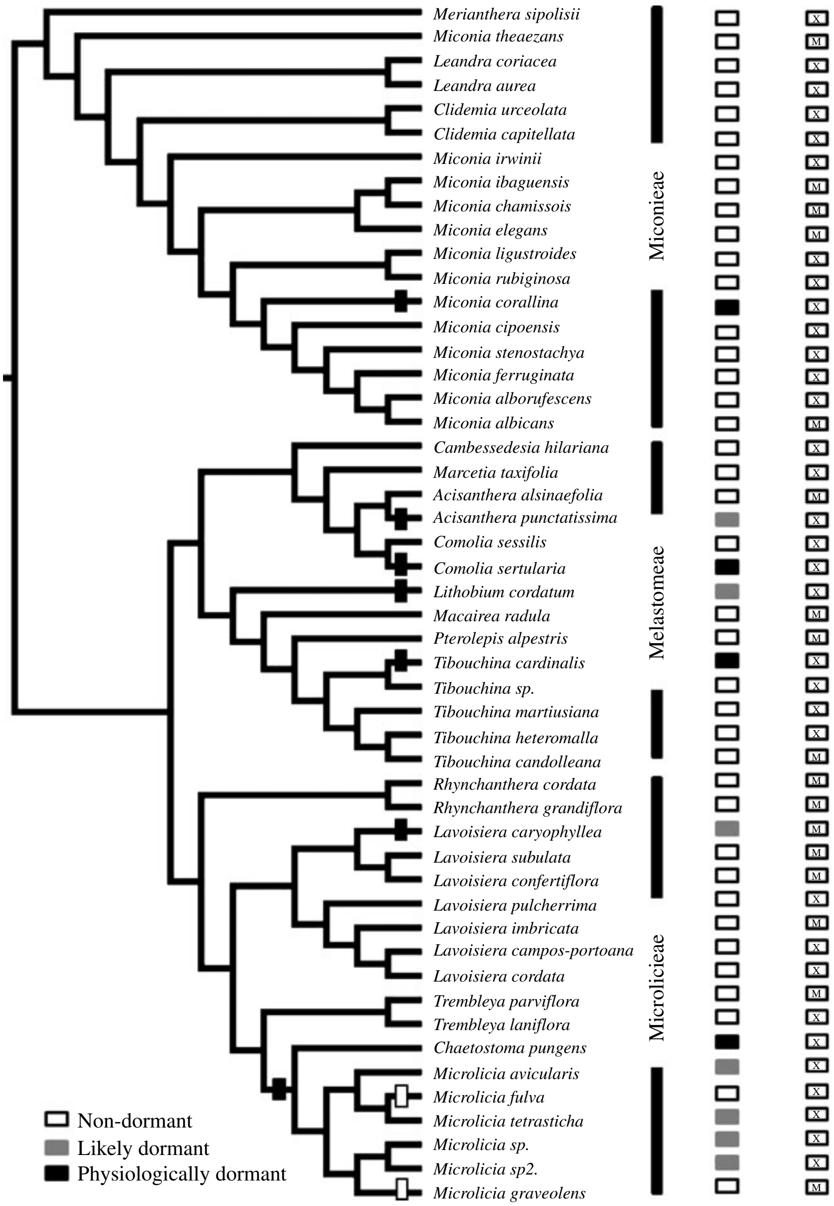

Figure 1. Reconstruction of the phylogenetic tree of 50 Melastomataceae species, showing non-dormant, likely dormant and dormant species. Filled dashes indicate the transition between non-dormant to dormant states and empty dashes indicate transition between dormant to non-dormant states. Species microhabitats are also shown as xeric (X) and mesic (M).

Tibouchina cardinalis (Melastomeae) and *Comolia sertularia* (Melastomeae) are endemic shrubs from the rupestrian fields of Minas Gerais, *Chaetostoma armatum* (Microlicieae) a common subshrub occurring in south-eastern and southern Brazil, and *Miconia corallina* (Miconieae) a common plant in the rupestrian fields in south-eastern Brazil. *Miconia* produces biotically dispersed berries, whereas the other species produce dry capsules that allow for abiotic dispersal. *Miconia*, *Comolia* and *Tibouchina* establish on rocky outcrops, whereas *Chaetostoma* establishes on dry grasslands. Soil moisture decreases significantly at the beginning of the dry season in these xeric microhabitats (Silveira, 2011). These species disperse seeds at the transition between rainy and dry seasons at Serra do Cipó and Serra do Cabral. *Miconia*, however, disperses fruits during mid-rainy season at PEI and colonizes a shrubby and relatively denser rupestrian field (Chiavegatto, 2005).

Seed collection and germination experiments

Ripe fruits of each *Tibouchina*, *Chaetostoma* and *Comolia* were collected at Serra do Cipó between April and June 2008, 2009 and 2010. For *Miconia*, seeds were collected in April 2009, April 2010 and May 2010.

Germination was conducted separately for *Miconia* seeds collected in 2010. Fruits of *Comolia* were also collected in July 2008 at Serra do Cabral and fruits of *Miconia* were collected in March 2010 at PEI.

Morphometric analyses (seed length and width) were performed on 50 seeds of each of the four species. Seeds were photographed with a stereomicroscope (Zeiss Stemi 2000-C, Zeiss, Oberkochen, Baden-Württemberg, Germany), and variables were measured using Zeiss AxioVision Rel 4.7 software. Seed viability was assessed on these four species by means of seed dissection and the tetrazolium test. Four replicates of 25 seeds were cut under a stereomicroscope and checked for embryo presence/absence. Further, the tetrazolium test was conducted for four replicates of 25 seeds with embryos. Cut seeds were soaked in Petri dishes containing a 1% solution of tetrazolium. The Petri dishes were wrapped in a double sheet of aluminium foil and incubated at 30°C. For all four species, staining required 24–48 h. After this period, seeds containing white or light red coloration were considered non-viable and seeds containing red or dark red coloration were considered viable.

Four replicates of 50 (25 for *Miconia*) seeds were set per treatment. Seeds were set to germinate in 9-mm Petri dishes on a double sheet of filter paper moistened with Nistatin solution (2%) to prevent fungal growth. The Petri dishes were incubated under constant temperatures of 15, 20, 25, 30 and 35°C at a 12:12 h light:dark cycle (photosynthetic photon flux density $= 26\,\mu\text{mol}\,\text{m}^{-2}\,\text{s}^{-1}$). For *Tibouchina*, *Chaetostoma* and *Comolia* seeds collected in 2008, experiments were carried out at all temperatures. In 2009 and 2010, experiments were repeated under the optimum temperature for each species. Experiments were performed only at 25°C for *Comolia* seeds collected at Serra do Cabral and for *Miconia* seeds collected in both years and sites. All melastome species studied to date are photoblastic (Silveira, 2011), so germination data for dark conditions are not shown here. Seed germination was monitored at 24-h intervals for 30 d, and seeds were considered germinated when radicle emergence was observed. Since our focus is on the dormant species, the results for the other 46 species will be presented in an accompanying paper.

For each treatment, mean germination time (MGT) was calculated by the equation:

$$\text{MGT} = \sum_{i=1}^{k} n_i t_i \Big/ \sum_{i=1}^{k} n_i$$

where n_i is the number of seeds germinated in the time i, t_i is the time from the start of the experiment to the ith observation and k is the time of last germination (Ranal and Santana, 2006).

Data in percentages were arcsin transformed, and tests for normality and variance equality were run prior to hypothesis-testing analysis. Whenever data met the assumptions of parametric statistics, differences among means were determined by analysis of variance (ANOVA) followed by Tukey test ($\alpha = 0.05$) for multiple comparisons. When data did not meet the assumptions of the parametric tests, statistical differences among means were determined by Kruskal–Wallis followed by Conover test. The same procedures were carried on for MGT data.

Seed coat permeability

Five to 10 replicates of recently collected seeds (25 each for *Comolia* and *Miconia* and 50 each for *Chaetostoma* and *Tibouchina*) were weighed on a digital balance. Seeds were soaked in tap water for 72 h at room temperature and reweighed. Seed permeability was determined by the increase in seed mass, and differences in percentage increase between seed mass of dried and soaked seeds were determined by paired *t*-test or Wilcoxon test.

Seed anatomy and histochemistry

Seeds of the four species were submitted to routine anatomical procedures. Fresh seeds were fixed, washed, dehydrated in ethanol series and infiltrated according to Paiva *et al.* (2011). Sections were stained, mounted and submitted to histochemical tests (see supplemental material, Seed anatomy and histochemistry, available online only at http://journals.cambridge.org).

Results

Seed biometry, viability and germination

Seeds of the four species are small; seed length ranged from 0.63 to 1.64 mm and width from 0.35 to 1.36 mm (Table 1). Dry seed mass ranged from 0.0013 mg in *Chaetostoma* to 0.023 mg in *Miconia*.

Germinability of all four species was low irrespective of year of collection (Fig. 2). However, germinability of *Miconia* seeds from PEI was significantly higher than that of seeds from Serra do Cipó (Fig. 2). For most experimental conditions, germination was not observed. These conditions were represented by extreme temperatures (15°C and 35°C) in *Comolia* and *Chaetostoma* and also in *Chaetostoma* seeds collected in 2009. Across all experiments, only a single seed germinated (mean germinability = 0.33%) for *Chaetostoma* 2010, *Comolia* 2009 and 2008 and *Tibouchina* 2010. For *Tibouchina* 2009, germinability was 16.7%.

Table 1. Mean seed length and seed width (±SD), percentage of embryoless seeds, viable embryos, non-dormant and dormant seeds in four Melastomataceae species from Neotropical montane savannas in south-eastern Brazil

Species	Seed length (mm)	Seed width (mm)	Embryoless seeds (%)	Viable embryos (%)	Non-dormant (%)	Dormant seeds (%)
Chaetostoma armatum	0.63 ± 0.08	0.35 ± 0.05	58	48	1.3	41
Comolia sertularia	0.85 ± 0.1	0.71 ± 0.07	50	73.4	4.5	45
Miconia corallina	1.64 ± 0.12	1.36 ± 0.18	41	28.8	1	54
Tibouchina cardinalis	0.72 ± 0.1	0.46 ± 0.08	61	52.3	9.5	30

Seed coat permeability

We found significant increases in seed mass following a 72-h imbibition period for all species (Table 2). Percentage increase in seed mass ranged from 46 to 75%; thus, all species produce seeds with permeable seed coats.

Ecological association of seed dormancy

We found an uneven distribution of dormant species regarding microhabitat and dispersal phenology (Table 3). There were significant associations of dormant species and xeric microhabitats ($\chi^2 = 5.02$; $P = 0.024$) and of non-dormant species with other phenologies ($\chi^2 = 16.37$; $P < 0.001$). Other phenologies include seed dispersal during the dry and rainy season, and during dry–rainy transitions (Silveira, 2011). Thus, seed dormancy was strongly related to both microhabitat and life history.

Seed anatomy and histochemistry

Mature seeds are exarillate and exalbuminous. In all species, the embryos appeared well developed, filling the whole seed cavity and showing a conspicuous embryonic axis and two fleshy cotyledons. In *Chaetostoma*, *Comolia* and *Tibouchina*, the embryo was curved, following the shape of the seeds, while the embryo of *Miconia* was folded, with cotyledons parallel to the embryonic axis (see supplementary Figure S1, available online only at http://journals.cambridge.org).

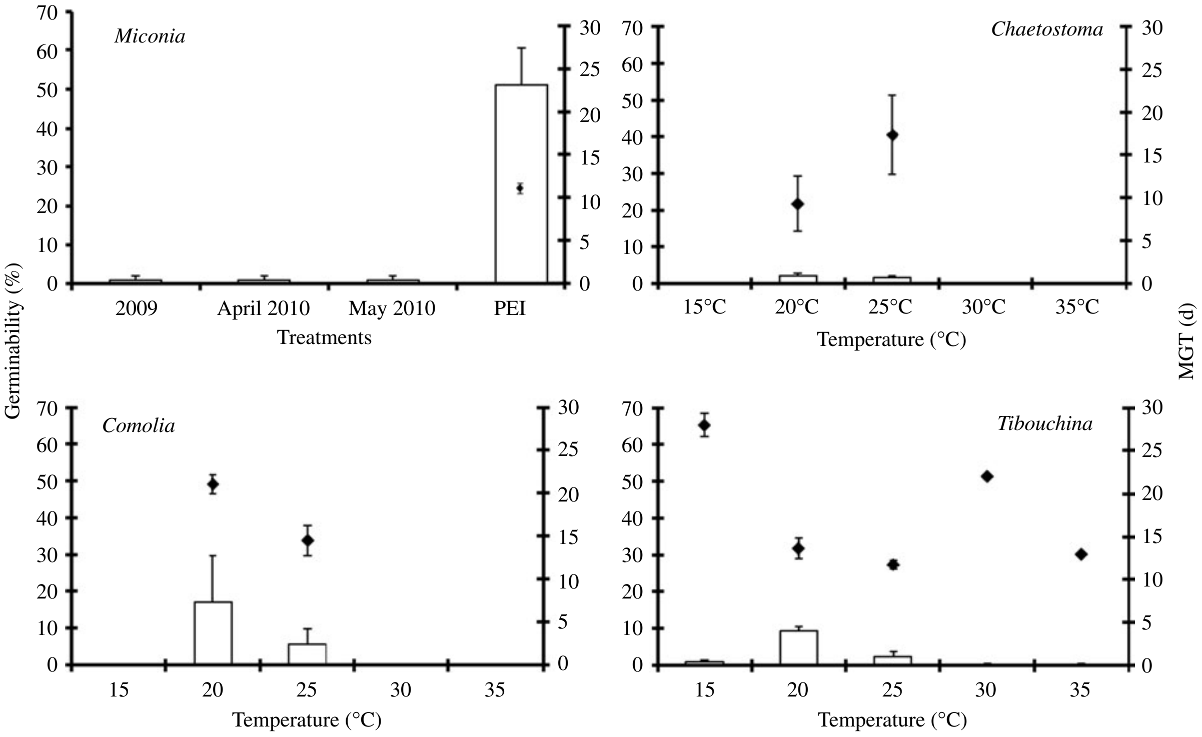

Figure 2. Mean (±SE) germinability (%, bars) and mean germination time [MGT (d), diamonds] of fresh seeds of *Miconia corallina*, *Tibouchina cardinalis*, *Comolia sertularia* and *Chaetostoma armatum* collected at Serra do Cipó and Parque Estadual do Ibitipoca (PEI).

Table 2. Seed mass before and after soaking in tap water for 72 h for four Melastomataceae species from Neotropical montane savannas in south-eastern Brazil. Statistics refer to Wilcoxon test for *Comolia* and paired *t*-test for the other species

Species	Seed mass (mg) before incubation	Seed mass (mg) after incubation	Statistics	Mean % increase
Chaetostoma armatum	0.0013	0.0019	7.6*	46.1
Comolia sertularia	0.00349	0.00509	45*	48.6
Miconia corallina	0.02322	0.03482	4.67*	55.4
Tibouchina cardinalis	0.00245	0.00428	13.87**	75.1

$^{*}P < 0.01$; $^{**}P < 0.001$.

Phylogenetic distribution of physiological dormancy

Based on the phylogenetic study, non-dormant seeds are assumed to be the ancestral condition and physiological dormancy (PD) is a derived character that was selected at least four times (once in Miconieae, once in Microlicieae and twice in Melastomeae; Fig. 1). Our data also suggest that seven additional species produce dormant seeds (Fig. 1).

Discussion

We have presented data showing that PD evolved at least four times during the history of Melastomataceae in the rupestrian fields. Although seed dormancy is thought to have evolved in melastomes from rainforest (Elisson *et al.*, 1993) and *cerrado* (Pereira-Diniz, 2003; Mendes-Rodrigues *et al.*, 2010), these previous studies do not present enough evidence to support the evolution of dormancy in tropical Melastomataceae. First, none of these studies included viability tests, so lack of germination may have been due to non-viable instead of dormant seeds. Moreover, none of these studies evaluated the frequency of embryoless seeds, which can be confounded with dormant seeds when seeds do not germinate. In addition, seeds of *Clidemia hirta* germinated to high percentages in a few days without any dormancy-breaking treatments (Pereira-Diniz, 2003), and low germinability in *M. ferruginata* is best explained by high percentages of embryoless seeds, rather than physical dormancy (seed coats were shown to be permeable; Mendes-Rodrigues *et al.*, 2010). Finally, dormancy-breaking treatments and germination promoters failed to increase germinability for those species. Our study represents the first unequivocal report on seed dormancy in tropical Melastomataceae.

Table 3. Frequency of dormant and non-dormant species in mesic and xeric sites in species shedding seeds during the rainy–dry transition and in other periods of the year

	Microhabitat		Phenology	
Dormancy status	Mesic	Xeric	Rainy–dry	Others
Dormant	1	11	9	3
Non-dormant	13	25	3	35

PD is the most common type of dormancy in the major clades of angiosperms and across vegetation types on Earth (Baskin and Baskin, 2005). The gain and loss of PD quite likely occurred many times during the evolution of seed plants (Linkies *et al.*, 2010), and our data suggest convergent evolution of PD in Melastomataceae. Nonetheless, we also present evidence for divergent evolution of dormancy in melastomes. Phylogeny-dependent evolution of seed dormancy is widely recognized (Baskin and Baskin, 2005) and may explain dormancy evolution. Dormancy appears to have evolved early in *Chaetostoma*–*Microlicia*, and for most *Microlicia* species reported here dormancy appears to be an ancestral (plesiomorphic) seed trait. The loss of dormancy in *M. graveolens* may have occurred prior to or after the transition of this species to mesic microhabitats and, thus, should be interpreted as a derived character.

Dormant and likely-dormant melastomes were associated with colonization of xeric microhabitats and with rainy-to-dry-season dispersal. Soil moisture is still high during the rainy-to-dry transition in xeric microhabitats of the rupestrian fields, but it drops significantly as the dry season approaches (Coelho *et al.*, 2006; Silveira, 2011). Small-rooted seedlings of these species would have to survive a forthcoming 4- to 5-month dry period before the perennial rains begin in October (Madeira and Fernandes, 1999). Therefore, we would expect high seedling mortality under these unfavourable (dry) conditions to be a strong selective pressure driving the evolution of seed dormancy. Drought-induced mortality is argued to be a strong and directional pressure favouring the evolution of PD in melastomes from the rupestrian fields. Therefore, avoiding germination at the rainy-to-dry transition can be an adaptive strategy delaying germination until the following rainy season.

Although we lack data to confidently assign dormancy for seven species, we assume they produce dormant seeds because these seeds are in the right place and time where dormancy evolved (see supplementary Table S1 and Table 3) and because embryoless seeds and non-viable embryos are insufficient to explain low germinability (Silveira, 2011). To be conservative, we assign seeds of these seven species to the likely dormant seed category. If future studies confirm seed dormancy in these seven species, three additional non-dormant-to-dormant transition events would be added.

Our data have important eco-evolutionary implications. First, they help us understand the biogeographical and phylogenetic distribution of seed dormancy across the global types of vegetation. Current estimates are that nearly 60% of tropical montane species have dormant seeds (Baskin and Baskin, 2005). We found 8% of the surveyed species had dormant seeds (percentage increases to 22% if dormancy is assigned in the other seven likely dormant species by future studies). Together with recent reports of seed dormancy in species from tropical montane vegetation (Gomes *et al.*, 2001; Silveira and Fernandes, 2006; Q.S. Garcia, pers. comm.), the data reported here suggest that seed dormancy in tropical montane vegetation was overestimated.

Second, our data provide key and practical information for predicting seed dormancy evolution in the *cerrado* flora. Previous models suggest that most seeds dispersed in the dry season are dormant, while most seeds dispersed in the wet season are non-dormant (Salazar *et al.*, 2011). We, on the other hand, have identified that the rainy-to-dry transition is the critical period for establishment in xeric microhabitats in the *cerrado* and that seed dormancy can be a central strategy to avoid germination when conditions are unlikely to remain favourable long enough for seedling establishment. However, microhabitat and phenology alone are not powerful predictors of seed dormancy. There are numerous species in xeric microhabitats in which dormancy has not evolved (see supplementary Table S1). On the other hand, species with rainy-to-dry transition dispersal are not necessarily dormant (see the case of the mesophyte *Miconia theaezans*). Therefore, the combination of phenology and microhabitat is a strong, but not universal, predictor of the evolution of seed dormancy in melastomes.

Another interesting example supporting our conceptual framework for the evolution of seed dormancy in tropical melastomes comes from among-population variation in seed dormancy in *M. corallina*. Individuals of *M. corallina* at PEI disperse their non-dormant seeds under favourable conditions for establishment. At Serra do Cipó, however, individuals dispersing seeds under unfavourable conditions produce dormant seeds. It is commonly accepted that among-population variation in seed dormancy and germination (Anderssen and Milberg, 1998; Lacerda *et al.*, 2004) is related to climatic conditions (Wagner and Simons, 2009). If this variation is genetically based (Lacerda, *et al.* 2004), microevolutionary changes would account for the evolution of locally adapted ecotypes. On the other hand, variation can also be the result of plastic responses mediated by maternal effects.

In summary, we have presented evidence for convergent evolution of PD in melastomes from Neotropical montane savannas. There is no reason to assume that multiple origins of seed dormancy would not explain the evolution of dormancy in other *cerrado* lineages. In contrast to tropical rainforest, the upper soil layers of seasonal vegetation have very negative soil water potential during the dry season (Coelho *et al.*, 2006; Salazar *et al.*, 2011), creating a suitable scenario for the evolution of seed dormancy. Therefore, we expect dormancy to have evolved in other taxa sharing similar microhabitats and life histories as those of dormant melastomes. Improving the predictability of the presence of seed dormancy has important implications for plant conservation, seed technology and restoration ecology.

Acknowledgements

We thank the grants and logistic support of the Conselho Nacional de Pesquisa (CNPq: 309633/2007-9, 304716/2008-1, 3057781/2009-9), Fundação de Amparo à Pesquisa do Estado de Minas Gerais (FAPEMIG: 697/06, EDT465/07, PPM 00182-10). We also thank N.C. Robles and N.M. Sales for help with laboratory experiments, N.F.O. Mota and M. Augsten for seed collection and L.C.S. Assis, R. Goldenberg and an anonymous reviewer for comments that significantly improved the quality of the manuscript. This study was in partial fulfilment of the PhD in Plant Biology requirements of F.A.O.S., who received scholarships from Coordenação de Aperfeiçoamento de Nível Pessoal Superior (CAPES), CNPq and FAPEMIG.

References

Alves, R.J.V. and Kolbek, J. (2010) Can campo rupestre vegetation be floristically delimited based on vascular plant genera? *Plant Ecology* **207**, 67–79.

Angiosperm Phylogeny Website (2011) Available at http://www.mobot.org/mobot/research/apweb/welcome.html (accessed 22 September 2011).

Anderssen, L. and Milberg, P. (1998) Variation in seed dormancy among mother plants, populations and years of seed collection. *Seed Science Research* **8**, 29–38.

Baskin, C.C. and Baskin, J.M. (2004) A classification system for seed dormancy. *Seed Science Research* **14**, 1–16.

Baskin, C.C., Baskin, J.M. and Chester-Edward, C. (1999) Seed dormancy and germination in *Rhexia mariana* var. *interior* (Melastomataceae) and eco-evolutionary implications. *Canadian Journal of Botany* **77**, 488–493.

Baskin, J.M. and Baskin, C.C. (2005) Classification, biogeography and phylogenetic relationships of seed dormancy. pp. 517–544 *in* Smith, R.D.; Dickie, J.B.; Linington, S.H.; Pritchard, H.W.; Probert, R.J. (Eds) *Seed conservation: turning science into practice*. London, Royal Botanic Gardens, Kew.

Chiavegatto B. (2005) A família Melastomataceae nos campos rupestres e cerrados de altitude do Parque Estadual do Ibitipoca, Lima Duarte, MG, Brasil. MSc dissertation, Jardim Botânico do Rio de Janeiro.

Clausing, G. and Renner, S.S. (2001) Molecular phylogenetics of Melastomataceae and Memecylaceae: implications for character evolution. *American Journal of Botany* **88**, 486–498.

Coelho, F.C., Capelo, C., Neves, A.C.O., Martins, R.P. and Figueira, J.E.C. (2006) Seasonal timing of pseudoviviparous reproduction of *Leiothrix* (Eriocaulaceae) rupestrian species in south-eastern Brazil. *Annals of Botany* **98**, 1189–1195.

Elisson, A.M., Denslow, J.S., Loiselle, B.A. and Brenes, D.M. (1993) Seed and seedling ecology of neotropical Melastomataceae. *Ecology* **74**, 1733–1749.

Finch-Savage, W.E. and Leubner-Metzger, G. (2006) Seed dormancy and the control of germination. *New Phytologist* **171**, 501–523.

Finkelstein, R., Reeves, W., Ariizumi, T. and Steber, C. (2008) Molecular aspects of seed dormancy. *Annual Review of Plant Biology* **59**, 387–415.

Giulietti, A.M., Pirani, J.R. and Harley, R.M. (1997) Espinhaço range region, eastern Brazil. pp. 397–404 *in* Davis, S.D.; Heywood, V.H.; Herrera-MacBryde, O.; Villa-Lobos, J.; Hamilton, A.C. (Eds) *Centres of plant diversity: a guide and strategy for their conservation*, *Vol. 3*. Cambridge, WWF/IUCN.

Gomes, V., Madeira, J.A., Fernandes, G.W. and Lemos-Filho, J.P. (2001) Seed dormancy and germination of sympatric species of *Chamaecrista* (Leguminosae) in a rupestrian field. *International Journal of Ecology and Environmental Sciences* **27**, 191–197.

Harper, J.L. (1977) *Population biology of plants*. London, Academic Press.

Hatschbach, G., Guarçoni, E.A.E., Sartori, M.A. and Ribas, O.S. (2006) Aspectos Fisionômicos da vegetação da Serra do Cabral, Minas Gerais, Brasil. *Boletim do Museu Botânico Municipal* **67**, 1–33.

Jacobi, C.M., Carmo, F.F., Vincent, R.C. and Stehmann, J.R. (2007) Plant communities on ironstone outcrops: a diverse and endangered Brazilian ecosystem. *Biodiversity and Conservation* **16**, 2185–2200.

Jurado, E. and Moles, A. (2002) Germination deferment strategies. pp. 381–388 *in* Nicolás, G.; Bradford, K.J.; Côme, D.; Pritchard, H.W. (Eds) *The biology of seeds: Recent research advances*. Wallingford, CABI Publishing.

Lacerda, D.R., Lemos-Filho, J.P., Goulart, M.F., Ribeiro, R.A. and Lovato, M.B. (2004) Seed-dormancy variation in natural populations of two tropical leguminous tree species: *Senna multijuga* (Caesalpinoideae) and *Plathymenia reticulata* (Mimosoideae). *Seed Science Research* **14**, 127–135.

Linkies, A., Graeber, K., Knight, C. and Leubner-Metzger, G. (2010) The evolution of seeds. *New Phytologist* **186**, 817–831.

Madeira, J.A. and Fernandes, G.W. (1999) Reproductive phenology of sympatric taxa of *Chamaecrista* (Leguminosae) in Serra do Cipó, Brazil. *Journal of Tropical Ecology* **15**, 463–479.

Medeiros, A.C., Loope, L.L., Conant, P. and McElvaney, S. (1997) Status, ecology and management of the invasive plant, *Miconia calvescens* DC (Melastomataceae) in the Hawaiian Islands. *Bishop Museum Occasional Papers* **48**, 23–36.

Mendes-Rodrigues, C., Araújo, F.P., Barbosa-Souza, C., Barbosa-Souza, V., Ranal, M.A., Santana, D.G. and Oliveira, P.E. (2010) Multiple dormancy and maternal effect on *Miconia ferruginata* (Melastomataceae) seed germination, Serra de Caldas Novas, Goiás, Brazil. *Revista Brasileira de Botânica* **33**, 93–105.

Mendonça, R.C., Felfili, J.M., Walter, B.M.T., Silva, M.C. Jr, Rezende, A.V., Filgueiras, T.S., Nogueira, P.E. and Fagg, C.W. (2008) Flora vascular do bioma Cerrado: checklist com 12.356 espécies. pp. 421–1279 *in* Sano, S.M.; Almeida, S.P.; Ribeiro, J.F. (Eds) *Cerrado: ecologia e flora*. Brasília, Embrapa Cerrados.

Meyer, J.-Y. and Florence, J. (1996) Tahiti's native flora endangered by the invasion of *Miconia calvescens* DC (Melastomataceae). *Journal of Biogeography* **23**, 775–781.

Oliveira-Filho, A.T. and Ratter, J.A. (2002) Vegetation physiognomies and woody flora of the cerrado biome. pp. 91–120 *in* Oliveira, P.S.; Marquis, R.J. (Eds) *The Cerrados of Brazil: Ecology and natural history of a Neotropical savanna*. New York, Columbia University Press.

Paiva, E.A.S, Pinho, S.Z. and Oliveira, D.M.T. (2011) Large plant samples: how to process for GMA embedding? pp. 37–49 *in* Chiarini-Garcia, H.; Melo, R.C.N. (Eds) *Light microscopy: Methods* and *protocols*. New York, Spinger/Humana Press.

Pereira-Diniz S.G. (2003) Ecofisiologia da germinação de sementes de *Clidemia hirta* (L.) D. Don (Melastomataceae). MSc dissertation, Universidade Federal de Uberlândia.

Ranal, M.A. and Santana, D.G. (2006) How and why to measure the germination process? *Revista Brasileira de Botânica* **29**, 1–11.

Ratter, J.A., Ribeiro, J.F. and Bridgewater, S. (1997) The Brazilian cerrado vegetation and threats to its biodiversity. *Annals of Botany* **80**, 223–230.

Renner, S.S. (2004) Bayesian analysis of combined chloroplast loci, using multiple calibrations, supports the recent arrival of Melastomataceae in Africa and Madagascar. *American Journal of Botany* **91**, 1427–1435.

Renner, S.S., Clausing, G. and Meyer, K. (2001) Historical biogeography of Melastomataceae: the roles of Tertiary migration and long-distance dispersal. *American Journal of Botany* **88**, 1290–1300.

Salazar, A., Goldstein, G., Franco, A.C. and Miralles-Wilhelm, F. (2011) Timing of seed dispersal and dormancy, rather than persistence in soil seed-banks, control recruitment of woody plants in Neotropical savannas. *Seed Science Research* **21**, 103–116.

Silveira F.A.O. (2011) Evolutionary ecophysiology of seed dormancy and germination of Melastomataceae from rupestrian fields. PhD thesis, Universidade Federal de Minas Gerais.

Silveira, F.A.O. and Fernandes, G.W. (2006) Effect of light, temperature and scarification on the germination of *Mimosa foliolosa* (Leguminosae) seeds. *Seed Science and Technology* **34**, 585–592.

Wagner, I. and Simons, A.M. (2009) Divergence in germination traits among arctic and alpine populations of *Koenigia islandica*: light requirements. *Plant Ecology* **204**, 145–153.