Dormancy in Seeds of Brazilian Cerrado and Dense Ombrophilous Forest

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ABSTRACT – The Cerrado and the Dense Ombrophilous Forest are important brazilian biomes that together cover more than half of the country's territory. They have a vast and rich plant diversity which often has a block in the germination process called dormancy. Dormancy can be defined as an obstruction in the germination of viable and intact seeds, even when all the favorable conditions are present. This work aimed to verify, through a literature survey, the occurrence of dormancy in seeds of plant species of the Brazilian Cerrado and Dense Ombrophilous Forest, comparing its occurrence between ecological groups of species, biomes and types of dormancy. The results showed that in Cerrado dormancy was observed in 56% of the species, whereas in Dense Ombrophilous Forest this number reduces to 42%. These data revealed an association between the presence of dormancy and the Cerrado. Also, in this biome, it was possible to verify a higher occurrence of physical dormancy in the seeds, with up to 63% of its dormant species presenting this type of dormancy. Pioneer species of Cerrado exhibited a greater dormancy percentage when comparing to climax, while this fact was not noticed in the forest, which resulted in an association between the ecological group of pioneer species from Cerrado and the dormancy process. These results show that dormancy may be related to more arid biomes and physical dormancy appears to be the most common type in these environments. Moreover, dormancy seems to be correlated with pioneer species of Cerrado, but not Forest.

Keywords: Biome; germination; savanna.

Dormência em Sementes do Cerrado e Floresta Ombrófila Densa Brasileira

RESUMO – O Cerrado e a Floresta Ombrófila Densa são importantes biomas brasileiros que juntos abrangem mais da metade do território nacional. Possuem uma vasta e rica diversidade vegetal que, muitas vezes, apresenta um bloqueio na germinação, chamado dormência. A dormência pode ser definida como um impedimento da germinação de sementes intactas e viáveis, mesmo quando as condições são favoráveis. Este trabalho teve por objetivo verificar, por meio de levantamento de dados, a ocorrência de dormência em sementes de espécies vegetais do Cerrado e da Floresta Ombrófila Densa brasileira, comparando sua ocorrência entre os grupos ecológicos de espécies, os biomas e os tipos de dormência. Os resultados mostraram que, no Cerrado, a dormência foi observada em 56% das espécies, enquanto na Floresta Ombrófila Densa, esse número reduziu para 42%. Esses dados revelaram uma associação entre a presença de dormência e o Cerrado. Ainda nesse bioma, foi possível verificar uma maior ocorrência de dormência física nas sementes, com até 63% de suas espécies dormentes apresentando esse tipo de dormência. As espécies pioneiras do Cerrado exibiram maior percentual de dormência em relação às espécies clímax, enquanto esse fato não foi percebido na floresta, o que resultou em uma associação entre o grupo ecológico das espécies pioneiras do Cerrado e o processo de dormência. Esses resultados mostram que a dormência pode estar relacionada a biomas mais áridos, e que a dormência física parece ser o tipo mais comum nesses ambientes. Ademais, a dormência parece estar correlacionada com espécies pioneiras do Cerrado, mas não com a Floresta.

Palavras-chave: Bioma; germinação; savana.

Dormancia en Semillas del Cerrado y Bosque Ombrofílico Denso Brasileño

RESUMEN – El Cerrado y el Bosque Denso Ombrófilo son importantes biomas brasileños que en conjunto cubren más de la mitad del territorio nacional. Tienen una vasta y rica diversidad que a

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menudo tiene un bloque de germinación llamado latencia. Latencia es define como un impedimento para la germinación de semillas intactas y viables, incluso cuando las condiciones son favorables. Este estudio tuvo como objetivo verificar, la ocurrencia de latencia en semillas de especies del Cerrado y el Bosque Denso Ombrófilo Brasileño, comparando su ocurrencia entre grupos ecológicos, biomas y tipos de latencia. Los resultados mostraron que, en el Cerrado, se observó latencia en el 56% de las especies, mientras que en el Bosque este número se redujo al 42%. Estos datos revelaron una asociación entre la presencia de latencia y el Cerrado. Asimismo, en este bioma se pudo constatar una mayor ocurrencia de latencia física en semillas, con hasta un 63% de sus especies latentes mostrando este tipo de latencia. Las especies pioneras del Cerrado exhibieron un mayor porcentaje de dormancia en relación a los clímax, mientras que este hecho no se notó en el bosque, lo que resultó en una asociación entre el grupo ecológico de especies pioneras del Cerrado y el proceso de dormancia. Estos resultados muestran que la latencia puede estar relacionada con biomas más áridos y que la latencia física parece ser el tipo más común en estos entornos. Además, la latencia parece estar correlacionada con las especies pioneras del Cerrado, pero no con el Bosque.

Palabras clave: Bioma; germinación; sabana.

Introduction

The Brazilian phytogeographic classification dates back to the 19th century, and these days comprises six important biomes in its territory. Among the many vegetation types found, the Dense Ombrophilous Forest stands out. Formerly named Rain Forest (IBGE, 2012), it has a vegetation dominated by high sized phanerogams, lianas and epiphytes. It is subjected to the occurrence of high temperatures, average 25°C, as well as high rainfall, around 1500 mm/year, well distributed throughout the year (Carvalho et al., 2013). The Amazon Forest and Atlantic Forest are the main examples of this vegetation and today occupies about 40% of the Brazilian territory (Almeida et al., 2010).

Another Brazilian characteristic vegetation is the Cerrado. Over the past two hundred years, this biome has received names from “estepe”, “savannah forest” and now the name Savanna is considered its major synonymous (Coutinho, 2006). The Cerrado is classified as the second largest Brazilian biome, occupying 21% of the national territory and has a seasonal climate, with a long dry season that lasts from April to September (Battle-Bayer et al., 2010).

Alongside the classification of Brazilian flora, the distribution of plant species found in these biomes in ecological groups features a wide range of groups. These classes arebasically divided in pioneers, early secondary, late secondary and climax (Kageama and Castro, 1989). Pioneer species are those with rapid growth, high requirement of light for seed germination, large production of small seeds throughout the year, as well as its high persistence in soil, that form seed banks in the soil due to what the studies believe to be the occurrence of a process called dormancy (Peres et al., 2009). Climax species, on the other hand, tend to have slow growth, low light requirement for seed germination and a low production of big seeds, which do not remain in the soil seed bank (Scremin Dias et al., 2006). Secondary species would be, in the majority of cases, in a middle ground between the two.

Seed dormancy can be defined as the failure of germination even when favorable conditions for their establishment and survival are offered (Finch-Savage and Leubner-Metzger, 2006). Among these conditions, water, oxygen and temperature can be highlighted. Dormancy in seeds is a complex process, present in a large number of wild species but little manifested in cultivars (Lenser and Theissen, 2013). It can be regulated by a number of factors, both environmental (temperature, light, humidity) or endogenous (hormonal balance, genetic mechanisms, epigenetic and molecular) (Graeber et al., 2012). It can be classified in many different categories but the two most easily found are Physiological, when there is a presence of inhibitory substances in the embryo, and Physical in which the seed integument becomes impermeable to water uptake (Baskin and Baskin, 2004). Analyzing the distribution of types of dormancy in tropical forest species worldwide have found a higher incidence of physiological dormancy in humid forest formations, whereas cases of physical dormancy increased as water availability decreased (Ferreira and Borguetti, 2009).

The literature demonstrates that the majority of studies that aimed the understanding of seed dormancy have been carried out in temperate areas (Baskin and Baskin, 2005). Therefore, studies that analyze this phenomenon in plants from tropical regions are extremely necessary. Thus, given the importance of the process of dormancy and its presence in tropical biomes, this work aimed to verify the occurrence of dormancy in seeds of plants from the Dense Ombrophilous Forest and the Brazilian Cerrado, and determine if there is a connection between the occurrence of the process, the biomes, ecological groups and the type of dormancy.

Materials and Methods

It was developed a bibliographic survey of the existing literature on dormancy in the Brazilian Cerrado and Dense Ombrophilous Forest species. The information about the presence or absence of dormancy was collected directly from publications or indirectly through data and/or techniques reported for storage and seed germination. The research was carried out using Scielo's databases, Periodicos Capes and books specializing in Brazilian plants. The species compileted were classified into Climax and Pioneer, using the criteria established by Maciel et al. (2003), which considers that the ecological classification of plant species is associated with the process of natural succession dynamics, with different characteristics from one group to another. In order to verify the dependence between the occurrence of dormancy, the different biomes, ecological groups and types of dormancy, the Chi-Square test of Pearson was used. The SPSS statistical package, version 20.0 was used and adopted a 5% significance level.

Results and Discussion

The present work presented a compilation of 110 plant species for the Cerrado and 110 for the Dense Ombrophilous Forest (Tables 1 and 2).

Table 1 – Dormancy occurrence in plant species of the Brazilian Cerrado.

Botanical family	Species	Ecological group	Dormancy	Break of dormancy	Ref
Anacardiaceae	*Anacardium occidentale* L.	Climax	Yes (Physical)	Water immersion for 48h	38, 42
	Anacardium giganteum W. Hancock ex Engl.	Climax	Yes (Physical)	Water immersion for 48h	40
	Myracrodruon urundeuva Allemão	Climax	Yes (Physiological)	Water immersion for 24 hours	49
	Schinopsis brasiliensis Engler.	Climax	Yes (Physical)	Scarification	44
Annonaceae	*Annona coriacea* Mart.	Pioneer	Yes (Physical)	Mechanical scarification	38
	Annona crassiflora Mart.	Pioneer	Yes (Physiological)	Post maturation with high temperature and humidity	44
	Cardiopetalum calophyllum Schltdl.	Pioneer	Yes (Physical)	Chemical or mechanical scarification	40
	Xylopia aromática (Lam) mart.	Pioneer	Yes (Physical)	Mechanical scarification	38
	Xylopia emarginata Mart	Pioneer	Yes (Physical)	Mechanical scarification	38
Apocynaceae	*Aspidosperma macrocarpon* Mart.	Climax	No	-	38
	Aspidosperma subincanum Mart.	Climax	No	-	45,46
	Aspidosperma tomentosum Mart. & Zucc.	Clímax	No	-	43
	Hancornia speciosa Gomes.	Climax	Yes (Physical)	Immersion in water followed by light	38
	Himatanthus obovatus (Mill. Ang.) Woodson.	Pioneer	Yes (Physiological)	Light, alternating temperatures or post maturation	40, 47

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Botanical family	Species	Ecological group	Dormancy	Break of dormancy	Ref
Araliaceae	*Schefflera macrocarpa* (Cham e Schltdl.) Frodin	Pioneer	No	-	40
Arecaceae	*Attalea oleifera* Barb.Rodr.	Clímax	No	-	138, 139
	Bactris setosa Mart.	Clímax	No	-	129
Asteraceae	*Dasyphyllum tomentosum* (Spreng)	Pioneer	Yes (Physiological)	Light or storage	48
	Eremanthus arboreus (Gardner) MacLeish	Pionner	Yes (Morphological)	Light	140
	Piptocarpha rotundifolia (Lass.) Baker	Pioneer	Yes (Physiological)	Light, alternating temperatures or post maturation	40
Bignoniaceae	*Jacaranda macrantha* Cham	Pioneer	No	-	51
	Cybistax antisyphilitica (Mart.) Mart	Pioneer	Yes (Physiological)	Light, alternating temperatures or post maturation	38,28
	Jacaranda cuspidifolia (Mart.)	Pioneer	No	-	45
	Tabebuia caraiba (Mart.) Bur.	Climax	No	-	125
	Tabebuia insignis (Miq) Sandwith.	Pioneer	No	-	38
Calophyllaceae	*Calophyllum brasiliense* Camb.	Climax	Yes (Physical)	Immersion in water for 24h	128
Cannabaceae	*Celtis pubescens* Spreng	Pioneer	No	-	40
Caryocaraceae	*Caryocar brasiliense* Camb.	Pioneer	Yes (Physical)	Immersion in water for 48h, with change every 12h.	38,53
Celastraceae	*Plenckia populnea* Reissuk.	Pioneer	No	-	45, 50
Chrysobalanaceae	*Couepia grandiflora* (Mart e Zucc) Benth ex Hock. F.	Climax	No	-	45
	Licania humilis Cham. e Schltde	Clímax	No	-	40
Clusiaceae	*Kielmeyera coriacea* Mart & Zucc	Pioneer	No	-	54, 55
	Kielmeyera variabilis Mart.	Pioneer	Yes (Physiological)	Light, alternating temperatures or post maturation	38, 28
Combretaceae	*Terminalia argentea* Mart e Zucc	Pioneer	Yes (Physiological)	Light, alternating temperatures or post maturation	38, 52
Dichapetalaceae	*Tapura amazônica* Poepp. & Endl.	Pioneer	Yes (Physical)	-	131
Dilleniaceae	*Curatella americana* L.	Pioneer	Yes (Morphophysiological)	Light	45, 56
	Davilla nitida (Vahl) Kubitzki	Pioneer	Yes (Morphophysiological)	Light, alternating temperatures or post maturation	57
Erythroxylaceae	*Erythroxylum suberosum* A.St.-Hil.	Pioneer	Yes (Morphophysiological)	Light	130
Euphorbiaceae	*Mabea fistulifera* Mart.	Pioneer	No	-	38

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Botanical family	Species	Ecological group	Dormancy	Break of dormancy	Ref
Fabaceae	*Bauhinia longifolia* (Bong.) Steud.	Pioneer	Yes (Physical)	Immersion in hot water	40,9
	Acacia mangium Willd.	Pioneer	Yes (Physical)	Immersion in boiling water	132
	Acacia paniculata Willd.	Pioneer	Yes (Physical)	Scarification	133
	Diptychandra aurantiaca Tul.	Climax	No	-	74
	Hymenoea stigonocarpa Mart. Ex. Hayme	Pioneer	Yes (Physical)	Mechanical scarification	38, 58
	Pentagyna confertiflora (Mart. Ex Hayme) Benth	Climax	No	-	40
	Tachigali rubiginosa (Mart. Ex Tul.) Oliveira Filho	Pioneer	Yes (Physical)	Mechanical scarification	40
	Albizia niopoides (Benth.) Burkart var. niopoides	Pioneer	Yes (Physical)	Water at 80°C for 3 minutes	38, 59
	Anadenanthera falcata (Benth.) Speg	Pioneer	No	-	38
	Chloroleucon tenuiflorum (Benth.) barneby e J.W. Grimes	Pioneer	Yes (Physical)	Mechanical scarification	40
	Dimorphandra mollis Benth.	Pioneer	Yes (Physical)	Mechanical scarification	38
	Enterolobium gummiferum (Mart.) J.F. Macbr	Climax	Yes (Physical)	Mechanical scarification	40
	Enterolobium timbouva Mart.	Pioneer	Yes (Physical)	Mechanical scarification	40
	Mimosa laticífera Rizzini & A. Mattos	Pioneer	Yes (Physical)	Mechanical scarification	40
	Plathymenia reticulata Benth.	Climax	Yes (Physical)	Chemical scarification	38,60, 61
	Stryphnodendron adstringens (Mart.) Canilla	Pioneer	Yes (Physical)	Chemical scarification with sulfuric acid for 60 minutes	38,62
	Acosmium subelegans (Mohlenbr) Yakovlev	Pioneer	No	-	38
	Bowdichia virgilioides Kenth.	Climax	Yes (Physical)	Chemical scarification with sulfuric acid	45,63
	Centrolobium tomentosum Guillemin ex Benth.	Pioneer	Yes (Physical)	Immersion in water at 25°C for 48 hours	38,64
	Dalbergia miscolobium Benth.	Pioneer	No	-	50, 65
	Dipteryx alata Vogel	Climax	Yes (Physical)	Mechanical scarification	38,66
	Machaerium acutifolium Vogel	Pioneer	No	-	38
	Platypodium elegans Vogel	Pioneer	Yes (Physical)	Longitudinal cuts in the pericarp	45,67
	Pterodon emarginatus Vogel	Climax	Yes (Physical)	Isolation of endocarp	68, 69
	Sclerolobium paniculatum Vogel	Pioneer	Yes (Physical)	Immersion in hot water	134
	Vatairea macrocarpa Ducke	Climax	Yes (Physical)	Mechanical scarification	38
Lamiaceae	*Aegiphila klotzschiana* Cham.	Pioneer	No	-	40
	Hyptidendron asperrimum (Spreng) R.M. Harley	Pioneer	No	-	40
	Vitex polygama Cham.	Pioneer	Yes (Physiological)	Light, alternating temperatures or post maturation	45

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Botanical family	Species	Ecological group	Dormancy	Break of dormancy	Ref
Lauraceae	*Ocotea corymbosa* (Meisn) Mez.	Pioneer	Yes (Physical)	Mechanical scarification	38,70
Lecythidaceae	*Cariniana estrellensis* (Rodd) Kuntze	Climax	No	-	38,21
	Cariniana rubra Gardner ex miers	Climax	No	-	40
	Eschweilera nana Miers	Pioneer	Yes (Physical)	Mechanical scarification	41
Lythraceae	*Lafoensia pacari* A. St. Hill	Pioneer	No	-	45,21
	Physocalymma scaberrimum Pohl	Pioneer	No	-	40
Malpighiaceae	*Byrsonima coriacea* (Sw.) DC	Pioneer	No	-	38,44
	Byrsonima intermedia A. Juss.	Pionner	Yes (Morpho Physiological)	Growing in culture media	141
Malvaceae	*Pseudobombax tomentosum* (Mart e Zucc) A. Rabyr	Climax	No	-	40,71
	Sterculia Striata A. St. Hill e Naudin	Pioneer	Yes (Physical)	Mechanical scarification	38,72
Marcgraviaceae	*Schwartzia adamantium* (Combess) Belell ex. Giraldo-Cañas	Climax	No	-	41,74
Melastomataceae	Miconia ligustroides DC Naudim	Pioneer	Yes (Physical)	Sulfuric acid for 5 min	75
	Tibouchina stenocarpa (DC.) Cogn.	Pioneer	No	-	38
Moraceae	*Brosimum gaudichaudii* Trécul	Clímax	No	-	142
Myristicaceae	*Virola sebifera* Aubl.	Pioneer	Yes (Physiological)	Light, alternating temperatures or post maturation	38,18
Myrsinaceae	*Rapanea guianensis* (Lam.) Lundell	Pioneer	Yes (Physiological)	Light, alternating temperatures or post maturation	76
Myrtaceae	*Eugenia dysenterica* DC.	Pioneer	Yes (Physical)	Mechanical scarification	44,77
	Gomidesia lindeniana O. Berg	Pioneer	Yes (Physiological)	Light, alternating temperatures or post maturation	40
Nictaginaceae	*Guapira graciliflora* (Schmidt) Lundell	Climax	No	-	40
	Neea theifera Oerst	Climax	No	-	124
Ochnaceae	*Ouratea spectabilis (Mart.)* Engl.	Pioneer	Yes (Physiological)	Light	143
Opiliaceae	*Agonandra brasiliensis* Miersex Benth. & Hook	Pioneer	Yes (Physical)	Scarification	135
Picrodendraceae	*Piranhea securinega* Radcl.-Sm. & Ratter.	Climax	No	-	44
Polygonaceae	*Coccoloba mollis* Casar.	Pioneer	No	-	40
Rhamnaceae	*Ziziphus joazeiro* Mart.	Pioneer	Yes (Physical)	Chemical scarification with sulfuric acid	44,78
Rubiaceae	*Coussarea hydrangeifolia* (Benth.) Benth e Hook ex. Mull Ang	Climax	Yes (Physiological)	Light, alternating temperatures or post maturation	38,74
	Rudgea viburnoides (Cham.) Benth	Climax	Yes (Physiological)	Light	127

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Botanical family	Species	Ecological group	Dormancy	Break of dormancy	Ref
Sapindaceae	*Diatenopteryx sorbifolia* Radlk	Pioneer	No	-	38
	Dilodendron bipinnatum Radlk	Pioneer	No	-	38
	Magonia pubescens A. St. Hill	Pioneer	No	-	38
	Matayba guianensis Aubl	Pioneer	No	-	125
Sapotaceae	*Pouteria ramiflora* (Mart.) Radlk	Climax	Yes (Physiological)	Light	74,126
Simaroubaceae	*Simarouba versicolor* A. St. Hil	Pioneer	Yes (Physiological)	Light, alternating temperatures or post maturation	40,28
Siparunaceae	*Siparuna brasiliensis* (Spreng.) A.DC.	Clímax	No	-	144
Solanaceae	*Solanum lycocarpum* A. st.Hil	Pioneer	Yes (Physical)	Mechanical scarification	40,79
	Solanum grandiflorum Ruiz & Pav	Pioneer	No	-	38
Styracaceae	*Styrax ferrugineus* Nees & Mart	Climax	Yes (Physiological)	Giberelic acid	38
Vochysiaceae	*Qualea dichotoma* (Mart.) Warm.	Pioneer	No	-	38
	Qualea multiflora Mart.	Pioneer	No	-	40
	Salvertia convallariodora A. st. Hill	Climax	No	-	38
	Vochysia tucanorum Mart.	Pioneer	No	-	38, 80
Winteraceae	*Drimys brasiliensis* Miers	Clímax	No	-	145

Table 2 – Dormancy occurrence in plant species of the Dense Ombrophilous Forest.

Botanical family	Species	Ecological group	dormancy	Break of dormancy	ref
Anacardiaceae	*Astronium concinnum* Schott ex Spreg	Climax	No	-	39
	Spondias venulosa (Engl.) Mart ex Engl.	Climax	No	-	39
	Spondias mombin L.	Climax	No	-	73
Annonaceae	*Annona cacans* Warm.	Climax	Yes (Morpho-physiological)	Post maturation	81
	Xylopsia brasiliensis Spreng	Pioneer	Yes (Physical)	Mechanical scarification	38, 82
	Xylopia frutescens Aubl	Pioneer	Yes (Physical)	Mechanical or chemical scarification	38, 83
Apocynaceae	*Aspisdosperma ramiflorum* Mull. Arg.	Climax	No	-	38
	Aspidosperma olivaceum Müll. Arg.	Climax	No	-	73
	Malouetia cestroides (Nees ex Mart.) Müll.Arg.	Pioneer	No	-	39
	Peschiera Fuchsiaefolia (A. DC.) Miers	Pioneer	No	-	38
Aquifoliaceae	*Ilex affinis* Gardner	Climax	Yes (Morpho-physiological)	Stratification	39
	Ilex paraguariensis Saint-Hilaire	Climax	Yes (Physiological)	Alternating light and temperature	49

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Botanical family	Species	Ecological group	Dormancy	Break of dormancy	Ref
Araliaceae	*Dendropanax cuneatum* (DC) Dechea Planch.	Climax	Yes (Physiological)	Light, alternating temperatureor post maturation	38,84, 7
Arecaceae	*Euterpe edulis* Mart.	Climax	No	-	117
	Syagrus romanzoffiana (Cham.) Glassman	Climax	No	-	136
Asteraceae	*Piptocarpha angustifolia* Dusén ex Malme	Pioneer	Yes (Physiological)	Light or alternating temperature	85, 137
Bignoniaceae	*Handroanthus heptaphyllus* (Vell.) Matts	Climax	No	-	127
	Jacarandá copaia (Aubl) D. Dan	Pioneer	No	-	86
	Paratecoma peroba (Record e Mell) Kuhlm.	Climax	No	-	87
	Zeyheria tuberculosa (Vell.) Bureau	Pioneer	No	-	38
Bixaceae	*Bixa orellana* L.	Pioneer	Yes (Physical)	Mechanical or chemical scarification	88, 89
	Bixa arborea Huber	Pioneer	No	-	90
Boraginaceae	*Auxemma oncocalyx* (Fr. All.) Baill	Climax	Yes (Physiological)	Light	73
	Patagonula americana L.	Pioneer	No	-	118,49
Burseraceae	*Trattinnickia rhoifolia* Willd	Climax	Yes (Physiological)	Light, alternating temperature or post maturation	94, 95
	Protium heptaphyllum (Aubl.) Marchand	Climax	No	-	73
Canellaceae	*Cinnamodendron dinisii* Schwacke	Climax	No	-	127
Cecropiaceae	*Cecropia hololeuca* Miq	Pioneer	Yes (Physiological)	Alternating temperature	38
	Cecropia glaziovii Sneth	Pioneer	Yes (Physiological)	Light, alternating temperature or post maturation	39, 96
	Pourouma guianensis Aubl.	Pioneer	No	-	39
Chrysobalanaceae	*Hirtella hebeclada* Moric. Ex DC.	Climax	No	-	97
	Licania tomentosa (Benth.) Fritsch	Pioneer	No	-	38
Clethraceae	*Clethra scabra* Pers	Pioneer	Yes (Physiological)	Light, alternating temperature or post maturation	39
Clusiaceae	*Garcinia brasiliensis* Mart	Climax	No	-	135
Combretaceae	*Terminalia kuhlmannii* Alman e Stace	Climax	Yes (Physiological)	Light, alternating temperature or post maturation	39
Cunoniaceae	*Lamanonia ternata* Vell	Pioneer	No	-	49

Botanical family	Species	Ecological group	Dormancy	Break of dormancy	Ref
Euphorbiaceae	*Alchornea iricurana* Casar	Pioneer	No	-	38
	Croton urucurana Baill	Pioneer	Yes (Morpho-physiological)	Thermal shock	98
	Hevea brasiliensis (Willd ex. A. Juss) Mull. Arg.	Climax	No	-	99
	Joannesia princeps Vell.	Pioneer	Yes (Physiological)	Gibberellic acid for 24 hours	100, 101
	Margaritaria nobilis L.f.	Climax	Yes (Physiological)	Light, alternating temperature or post maturation	39
	Sebastiania commersoniana (Baill.) L.B. Sm. & Downs	Pioneer	No	-	38
Fabaceae	*Apuleia leiocarpa* (Vogel) J.F. Macbr	Climax	Yes (Physical)	Hot water or chemical scarification	102
	Bauhinia fortificata Link	Pioneer	Yes (Physical)	Mechanical scarification	38
	Caesalpinia echinata Lam.	Climax	No	-	103
	Holocalyx balansae Micheli	Climax	No	-	38
	Lonchocarpus muehlbergianus Hassl.	Pioneer	No	-	73
	Schizolobiumparahyba (Vell.) S.F. Blake	Pioneer	Yes (Physical)	Mechanical scarification and cold water	38
	Sclerolobium densiflorum Bentham	Climax	Yes (Physical)	Mechanical scarification	73
	Senna macranthera (DC. ex Collad.) H.S. Irwin & Barneby	Pioneer	Yes (Physical)	Mechanical or chemical scarification	121
	Senna multijuga (L.C. Rich.) Irwin & Barneby	Pioneer	Yes (Physical)	Mechanical or chemical scarification	121
	Senna pendula H. S. Irwin & Barneby	Pioneer	Yes (Physical)	Mechanical scarification	122
	Abarema jupunba Willd. Britton e Killip	Pioneer	Yes (Physical)	Mechanical scarification	39
	Albizia inundata (Mart.) Barneby & J.W Grimes	Pioneer	Yes (Physical)	Scarification	104, 127
	Anadenanthera colubrina (Vell.) Brenon	Pioneer	No	-	105
	Balizia pedicellaris (DC.) Barneby & J.W.Grimes	Pioneer	Yes (Physical)	Mechanical scarification	39
	Enterolobium contortisiliquum (Vell.) Morang	Pioneer	Yes (Physical)	Mechanical scarification	38
	Goldmania paraguariensis (Benth) Brenon	Pioneer	No	-	39
	Inga edulis Mart	Pioneer	No	-	106
	Mimosa bimucronata (DC.) Kuntze	Pioneer	Yes (Physical)	Immersion in water at 80 ° C or sulfuric acid for 5 min	107
	Pentaclethra macroloba (Wild.) Kuntze	Pioneer	No	-	39
	Andira fraxinifolia Benth	Pioneer	No	-	108
	Dalbergia nigra (Vell.) Allemao ex. Benth.	Climax	No	-	38
	Deguelia hatschbachii Tozzi	Pioneer	No	-	39
	Erythrina speciosa Andrews	Pioneer	Yes (Physical)	Chemical scarification	109
	Machaerium scleroxylon Tul.	Climax	No	-	49
	Myroxylon peruiferum L.f.	Climax	Yes (Physical)	Mechanical scarification	38
	Swartzia Longsdorffii Raddi	Climax	No	-	38

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Botanical family	Species	Ecological group	Dormancy	Break of dormancy	Ref
Flacourtiaceae	*Casearia sylvestris* Sw.	Pioneer	No	-	73
Humiriaceae	*Vantanea compacta* (Schnizl.) Cuatrec.	Climax	No	-	39
Icacinaceae	*Paraqueiba sericea* Tulasne	Climax	No	-	39
Lauraceae	*Aniba firmula* (Nees & Mart. ex Nees) Mez	Climax	Yes (Physiological)	Light or alternating temperatures	39
	Cinnamomum glaziovii (Mez) Kosterm	Climax	Yes (Physiological)	Light or alternating temperatures	39
	Mezilaurus crassiramea (Meisn.) Taub. ex Mez	Climax	Yes (Physiological)	Light or alternating temperatures	39
	Mezilaurus itauba (Meisn.) Taub. ex Mez	Climax	Yes (Physiological)	Post maturation	127
	Ocotea catharinensis Mez	Climax	No	-	38
	Persea pyrifolia Nees	Climax	No	-	73
Lecythidaceae	*Bertholletia excelsa* Kunth	Climax	Yes (Physiological)	Phenylmercury acetate (0,2%)	110, 111
	Cariniana estrellensis (Raddi) Kuntze	Climax	No	-	38
	Gustavia augusta L.	Climax	Yes (Physiological)	Light, alternating temperatures or post maturation	112
	Eschweilera coriacea (DC.) Mori	Climax	Yes (Physiological)	Light, alternating temperatures or post maturation	39
	Lecythislurida (Miers) S.A. Mori	Climax	Yes (Physiological)	Light, alternating temperatures or post maturation	38
Magnoliaceae	*Talauma ovata* A. St.-Hilaire	Climax	No	-	119
Malvaceae	*Bombacopsis glabra* (Pasq.) A. Rabys.	Pioneer	No	-	91
	Ceiba pentandra (L.) Gaertn.	Pioneer	No	-	57
	Luehea divaricata Mart. et Zucc	Pioneer	No	-	118
	Luehea candicans Mart. et Zucc.	Pioneer	No	-	73
	Ochroma pyramidale (Cav. Ex Lam.) Urb.	Pioneer	Yes (Physical)	Mechanical or chemical scarification	92, 93
	Spirotheca passifloroides Cuatrec	Climax	No	-	39
Melastomataceae	*Tibouchina pulchra* Cogn	Pioneer	No	-	39
	Tibouchina mutabilis Cogn	Pioneer	No	-	38
	Miconia cinnamomifolia (DC.) Naudin	Pioneer	Yes (Physiological)	Light	120
Meliaceae	*Cedrela odorata* L.	Pioneer	No	-	16, 86
Myristicaceae	*Virola oleifera* (Schott) A. C. Smith.	Climax	No	-	38
Myrtaceae	*Blepharocalyx salicifolius* (Kunth) O. Berg	Climax	No	-	38
	Eugenia uvalha Cambess	Climax	Yes (Physiological)	Gibberellic acid	113
	Plinia edulis (Vell.) Sobral	Climax	Yes (Physiological)	Light,alternating temperatures or post maturation	38
	Psidium cattleianum Sabine	Pioneer	Yes (Physiological)	Light	38

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Botanical family	Species	Ecological group	Dormancy	Break of dormancy	Ref
Nyctaginaceae	*Andradea floribunda* Allemao	Pioneer	No	-	39
	Ramisia brasiliensis Oliver	Pioneer	No	-	39
Phytolaccaceae	*Gallesia integrifolia* (Spreng) Horns	Pioneer	No	-	114
Proteaceae	*Euplassa cantareirae* Sleumer	Climax	No	-	39
	Roupala brasiliensis Klotzsch	Climax	No	-	49
Rhamnaceae	*Colubrina glandulosa* Perkins	Pioneer	Yes (Physical)	Mechanical or chemical scarification	123
Rubiaceae	*Isertia hypoleuca* Benth	Pioneer	Yes (Physiological)	Light, alternating temperatures or post maturation	39
Rutaceae	*Dictyoloma vandellianum* A. Juss.	Pioneer	No	-	115
	Neoraputia alba (Nees& Mart.) Emmerich	Climax	No	-	39
Salicaceae	*Salix humboldtiana* Willd.	Pioneer	No	-	49
Sapindaceae	*Allophylus edulis* (A.St.Hil. Cambess e A.Juss) Radlk	Pioneer	No	-	38
Sapotaceae	*Manilkara huberi* Chevalier	Climax	Yes (Physical)	Mechanical scarification	116

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In the Cerrado, dormancy was observed in 56% of the species. In contrast, the occurrence of dormancy in the seeds of the forest was 42% (Table 3). A statistical association between biomes and the presence of the dormancy phenomenon was evidenced (χ^2 = 4,09; p = 0.05).

Table 3 – Dormancy occurrence in plant seeds of Brazilian Cerrado and Dense Ombrophilous Forest.

Biome	Dormancy	Nondormancy	Total
Cerrado	62	48	110
Forest	47	63	110

It was observed a greater incidence of dormancy in Cerrado plants in comparison to the Dense Ombrophilous Forest. This was confirmed by Baskin and Baskin (2005), who analyzed 2040 tropical plant species and also found a higher percentage of species whose seeds had dormancy in savannah in relation to the rainforest. Jurado and Flores (2005) also conclude that the driest environments have greater probability of species dispersing dormant seeds. Sautu et al. (2007) had similar results in their analysis of the seeds of a tropical rainforest of Panama where they found less than 50% of dormant seeds. Emphasizing the importance of water for germination, Sautu et al. (2007) found that only 38% of species scattered in the forest at the beginning of the rainy season were dormant. However, for plants whose dispersion occurred at the end of the rainy season, the percentage of dormant seeds rose to 58%. Therefore, there is a clear combination of the rise of dormancy and absence of water. The water proves to be crucial and a limiting factor in the germination process, acting directly on the seed hydration and metabolic reactivation and providing the development of the embryo (Bewley et al., 2013).

Some authors consider that in forest, due to high ambient humidity conditions and higher water content in the seeds, the absence of dormancy is more likely than in the Cerrado species, which, in turn, have greater longevity (Vásquez-Yanes et al., 1993). The reasons why the dormancy is present in forests is not yet elucidated, however it is believed that it is more related to dispersion than any other factor (Souza et al., 2015). It is also proposed that the forest environment is presented not as homogeneous and predictable, where the opening of gaps brings important changes in light, humidity and ambient temperature, so mechanisms that can elevate that survivor rate would be an advantage (Volis and Bohrer, 2013). The rainforests may present then favorable and unfavorable periods to the plant establishment after germination, and the dormancy would have a crucial role in this case, although this process achieved 42% of the species of the biome in this work and was not significantly statistical. In the more adverse and unfavorable environmental conditions, as those presented in the Cerrado, due to the lower availability of water and the occurrence of aggravating events such as fire, common in the region, the chance to success in the germination becomes quite variable. This will result in a selective pressure in the plants, favoring the process of dormancy, as the seed persistence in soil provided by dormancy prevents it germinates in an unfavorable period to seedling establishment (Dalling and Brown, 2009; Salazar et al., 2011). It is known that the vast majority of the Cerrado species germinates quickly in the beginning of the wet season (Oliveira and Silva, 1993; Brancalion et al., 2010) and other authors confirm that 75% of species dispersed in the savanna dry season had dormancy, contrasting with the 43% found in the wet season (Salazar et al., 2011). Thus, it was expected a higher occurrence of dormancy in the Cerrado biome, which was observed in this study.

When analyzing the relationship between types of dormancy and biomes, the presence of a large number of species classified as physical or physiological was noticed. There was a significant association between the occurrence of physical dormancy and the Cerrado ($\chi^2 = 5{,}39$; $p = 0.05$). This biome presented physical dormancy in 63% of its analyzed dormant species (Table 4).

Table 4 – Types of dormancy in plant seeds of Brazilian Cerrado and Dense Ombrophilous Forest.

Biome	Physical dormancy	Physiological dormancy	Total
Cerrado	39	18	57
Forest	20	24	44

Physical dormancy is characterized by an impermeable seed coat resulting of impermeable layers that develop during maturation and drying of the seed or fruit (Paulsen et al., 2013). It is the second most common kind of dormancy and is present from herbs to trees in arid to tropical regions, although savannahs tend to have it more frequently (Baskin and Baskin, 2014). It has been proposed that this hard seededness protects against a high number of damaging factors, extends the seed longevity and persistence in soil seed banks (Paulsen et al., 2013). Moreover, this

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type of dormancy would also limit the entrance and loss of water to the environment, and it is a strategy that would increase the chances of success in the fight against pathogens (Dalling et al., 2011). The Cerrado is an environment with a well-defined high adverse drought period during the year and tends to present in its plants adaptive strategies to minimize the adverse effect of climate. The information found in this work for this biome confirms the results reported by Baskin and Baskin (1998), who in their studies on dormancy and physiognomy of tropical biomes have noted an increase in the percentage of physical dormancy in species as the environmental water availability is restricted or reaches arid or semi-arid areas. This corroborates the importance of water for germination, favoring the seeds that have mechanisms that protect themselves from the hard conditions of the ambient. Other important fact in this work is the existence of a vast number of plants from the Fabaceae family, known to have a higher incidence of physical dormancy (Baskin and Baskin, 2000; Funes and Venier, 2006). In a study from Baskin and Baskin (2005) involving a review of over 2,000 species of various phytophysiognomies, they found that 32% of the 192 species of Fabaceae from humid environment presented dormancy. The number grows in the savannah, with 68% of dormancy, especially physical, in the 93 species of the family. Dormancy is a hereditary characteristic in the family Fabaceae and although not yet fully elucidated its evolutionary origin, it is believed that might have arisen in response to competition of individuals of the same species initially, to avoid the conflict (Willis et al., 2014).

When verifying the relationship of dormancy with the ecological groups of the species, it was found that 63% of the pioneer species of the Cerrado were dormant. This number reduces to 43% when the climax plants are analyzed (Table 5). Applying the chi-square test, it was found an association between pioneer species and dormancy (χ^2 = 3,9; p = 0.05). However, in the Dense Ombrophylous Forest, no association was found for this parameter (Table 6). Only 44% and 41% of the pioneer and climax species respectively had dormancy (χ^2 = 0,06; p = 0.8).

Table 5 – Dormancy occurrence in pioneer and climax plant species of the Brazilian Cerrado.

Ecological group	Dormancy	Nondormancy	Total
Pioneer	46	27	73
Climax	16	21	37

Table 6 – Dormancy occurrence in pioneer and climax plant species of the Dense Ombrophylous Forest.

Ecological group	Dormancy	Nondormancy	Total
Pioneer	25	32	57
Climax	22	31	53

Several pioneer species have mechanisms that can both restrict and/or block the germination (Dalling and Brown, 2009). This restriction is believed to be caused mainly by dormancy in their seeds, which are small, though numerous and allows the formation of a persistent soil seed bank, where it requires light to germinate and tolerate desiccation (Peres et al., 2009). According to Bonner (1990) and Thusithana et al. (2018), climax species tolerate shade during germination and tend to be more sensitive to desiccation, not having long-term viability in the soil seed banks; thus, the dormancy does not seem to be advantageous. Moreover, they present seasonal behavior in seed production. The high dormancy percentage expected associated with pioneer species is related then to its orthodox behavior that can cause germination to be extended for a period of several years without damaging the quality of seeds, which remain viable in the soil seed banks, playing an important role in the restoration of environments (Long et al., 2015). This was confirmed by Dalling

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and Brown (2009) when studying the persistence of pioneer dormant species on soil seed bank, noticed the high recoverability of *Zanthoxylum ekmannsi* (Urb.) Alain, *Trema micrantha* (L.) and *Croton billbergianus* (Mull. Arg.) which germinated after 18, 31 and 38 years in the soil seed bank, respectively. Moreover, working with 14 Cerrado species of these two ecological groups, Salazar et al. (2011) found that specimens of pioneer species could reach a longevity of up to 26 months, contrasting with the poor viability of climax species. Additionally, similar results for the Cerrado were found when Colado et al. (2020) worked with the pioneer *Hymenaea stigonocarpa*, in which the dormancy started to be overcome and the germination increased significantly after the seed remained 6 months on the ground. The sample of the species in this work, for the Cerrado, indicate a correlation between the presence of dormancy and the ecological group of the species, in this case the pioneers. More than half of its species displayed this characteristic, contrasting with the low percentage verified in the climax species, which confirms the data found in the literature. Thus, this behavior found for pioneer species in this biome seems to be linked to the composition of the soil seed bank and its survival in tough dispersal times, which are found in a seasonal climate region with a long dry season condition. It is also known that for biomes with well-established drought conditions, key factors like the season, dispersing during the rainy-to-dry season, and the type of dispersion, i.e. the autochory, may play a strong contribution to the establishment of dormancy (Kuhlmann and Ribeiro, 2016; Escobar et al., 2018). This process, then, would be evolutionarily influenced by these variables but would be significantly associated with the pioneer species of the Cerrado. Therefore, this group of species may have been linked strategically to dormancy, ensuring the success in the dispersal of the seeds, which can guarantee a recomposition of the environment.

However, for the Dense Ombrophylous Forest, the species presented in this work did not indicate the existence of a correlation between dormancy and the ecological group of the species. Other recent studies that addressed biomes with similar characteristics also did not find relation between these two variables (Jurado and Flores, 2005; Souza et al., 2015). This non-association found for these ecological groups in this biome can be attributed to the fact that the control of germination may be associated not only to the light and shadow patterns, but in response to the genome, molecular and environmental factors, which many times are not constant. The fluctuations in aspects such as temperature, water, nutrients, types of dispersion and allelochemicals, which can be highly active in the forest, can also strongly influence the dormancy level (Finch-Savage; Leubner-Metzger, 2006). Moreover, the time that a species can persist in the soil from more humid locations may vary, sometimes, beyond the ecological group and the presence of dormancy process from the mother plant. Its interaction with biotic and abiotic environmental factors and the more homogeneous climatic conditions during the year may resulted in the establishment of a dormancy process that is not restricted to any ecological group, thus configuring an extraordinarily complex process (Long et al., 2015; Carrillo-Barral et al., 2020). This can be confirmed by Dalling et al. (1997), when studying exclusively pioneer species in rainforests of Panama, who noted a vast complexity as well as phenological characteristics in the analyzed plants and it´s seeds, which can corroborate this idea. Therefore, it can be inferred that the presence of dormancy may not be faithfully attributed to either ecological groups in rainy forests. Hence, by the analysis of the results in this work it can also be considered that the use of ecological group variable would preferably be associated with dormancy in pioneer species from drier biomes, in this case the Cerrado.

Conclusions

Seed dormancy is related to several types of plants and habitats, however, more arid environments tend to have a higher occurrence of this process. Physical dormancy appears to be the most common type in the aridest biome, the Cerrado. The phenomenon of dormancy cannot be attributed specifically to pioneer or climax species in the Dense Ombrophylous Forest, but it is presented more prominently in pioneer species from the Cerrado.

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