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Do seedling functional groups reflect ecological strategies of woody plant species in Caatinga?

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ABSTRACT

It is assumed that morphological traits of seedlings reflect different strategies in response to environmental conditions. The ecological significance of this has been widely documented in rainforests, where habitat structure and species interactions play an important role in community assembly. However, in seasonally dry ecosystems, where environmental filtering is expected to strongly influence community structure, this relationship is poorly understood. We investigated this relationship between functional groups of seedlings and life history traits and tested whether functional group predicts the ecological strategies employed by woody species to deal with the stressful conditions in seasonally dry ecosystems. Seedling functional groups, life history traits and traits that reflect ecological strategies for occupying seasonally dry environments were described for twenty-six plant species. Seedlings of species from the Caatinga vegetation exhibited a functional profile different from that observed in rainforests ecosystems. Phanerocotylar-epigeal seedlings were the most frequently observed groups, and had the largest range of ecological strategies related to dealing with seasonally dry environments, while phanerocotylar-hypogeal-reserve seedlings exhibited an increase in frequency with seasonality. We discuss these results in relation to those observed in other tropical forests and their ecological significance in seasonally dry environments.

Keywords: dry forest, environmental filtering, functional traits, initial establishment, recruitment, seasonality

Introduction

Approaches using functional groups have been successfully used in ecology as effective methods for synthesising patterns within and among communities and for describing mechanisms related to abiotic factors and biotic interactions based on the morphological and physiological traits of species (Cornelissen 2003; Lavorel 2007). Functional groups are defined as sets of species showing similar responses to environmental conditions, with similar effects on ecosystem functioning (Díaz & Cabido 2001). This approach seems to be especially useful in simplifying the complexity of species-rich communities and to relate species traits and adaptive strategies for certain environmental conditions.

Earlier studies have suggested that the variation in seedlings' cotyledon traits may reflect different establishment strategies among woody species (Vogel 1980; Garwood 1996). Seedling traits may play a role in the establishment of juveniles, since this stage is a critical phase in the life cycle and for the reproductive success of plants. Different systems have been proposed to classify seedling stages based on functional morphology (Ng 1978; Vogel 1980;

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Miquel 1987). More recently, Garwood (1996) reviewed these systems and proposed a broader classification, combining three characteristics from cotyledons: exposure (phanerocotylar – exposed/ cryptocotylar – hidden), position (epigeal – hypocotyl developed with elevated cotyledon/ hypogeal – cotyledon under or at ground level) and texture (foliaceous - main function of photosynthesis/ reserve – fleshy). Such combinations include five possible morpho-functional groups of seedlings likely to occur in nature: Phanerocotylar-Epigeal-Foliaceous (PEF), Phanerocotylar-Epigeal-Reserve (PER), Phanerocotylar-Hypogeal-Reserve (PHR), Cryptocotylar-Epigeal-Reserve (CER) and Cryptocotylar-Hypogeal-Reserve (CHR).

Overall, these functional groups of seedlings can reflect the different strategies that plant species use for their initial establishment (Kitajima 1996; Garwood 1996; Baraloto & Forget 2007). For example, PEF seedlings generally develop from small seeds with small reserves, thus resulting in quick development and rapid colonisation in the early stages of succession. In contrast, CHR seedlings generally come from large seeds with large reserves and slow development associated with later successional stages (Ng 1978; Hladik & Miquel 1990). Furthermore, groups of seedlings have different light requirements, with PEF seedlings able to grow fast in high light environments compared to CHR seedlings, which are more strongly associated with light-limited environments (Kitajima 1996). Additionally, seedlings with foliaceous cotyledons grow faster than species with reserve-type cotyledons, but survival after disturbances like grazing is five times higher in hypogeal cotyledons (Baraloto & Forget 2007).

Previous studies have shown that there is evolutionary convergence at the community level worldwide in these seedling traits (Ibarra-Manríquez 2001; Zanne *et al*. 2005), and a higher frequency of PEF and CHR seedling groups in Neotropical rain forests and of PHR, CER, and PER groups in moist Paleotropical regions (Ibarra-Manríquez 2001). However, little is known regarding the patterns of these functional groups with respect to decreasing rainfall. Especially in environments that experience strong seasonality, where the most limiting resource becomes water availability instead of light, and the role of species interactions in modulating community assembly is assumed to be less strong than in wet forests.

In markedly seasonal environments, community assembly is likely to be mediated more by environmental filtering than by biotic interactions (Grime 2006). Consequently, in such areas some species' functional traits tend to be more conservative and genetically fixed. These species are thus expected to vary less between ontogenetic stages, since trait variations caused by environmental conditions are greater than those caused by ontogeny (Fu *et al.* 2013). For example, some traits such as wood density, leaf matter dry content and water potential are more stable and, at least in respect to species' rank, tend to be more consistent across ontogenetic stages (Kitajima & Poorter 2010). As a result, some plant traits can be useful for gaining a better understanding of the ability of species to successfully establish in environments with strong filtering forces.

In Brazil, studies involving the functional morphology of native plant seedlings are strictly limited to a few species from the Cerrado, the Atlantic Forest and the Amazon floodplain (Ressel *et al.* 2004; Leonhardt *et al.* 2008; Feitoza *et al*. 2014). This information is even scarcer for dry tropical forests, with studies restricted to species of economic value and failing to address functional components (Cunha & Ferreira 2003; Feliciano *et al*. 2008). Since plants respond to environmental factors through a series of morphological, physiological or phenological traits, which impact growth, reproduction and survival (Violle *et al.* 2007), the seedling stage represents the most critical phases of a plant's life cycle, and these can determine the regenerative processes in plant communities.

Here, we investigated the above mentioned associations between functional groups of seedlings and ecological strategies of plants in the Caatinga, a seasonally dry tropical forest in the northeast of Brazil. We predicted that favorable seasonally conditions for recruitment and growth for plant species recorded in this semi-arid region will play a preponderant role in the occurrence of different functional groups when compared to other tropical forests. To address these issues, we first investigated if functional groups of seedlings are related to features of the life histories of plants. Afterwards, we contrasted these functional groups of seedlings with plant traits that reflect the ecological strategies of plants with regard to markedly seasonal environments, and we compared the patterns found to those from other tropical forests.

Materials and methods

Study area

This study took place in the Mata da Pimenteira State Park (7°89'S 38°30'W), located near Serra Talhada municipality, Pernambuco state, northeastern Brazil. The nature reserve covers an area of about 887 ha of seasonally dry tropical forest, locally called Caatinga vegetation. In this semi-arid region, rainfall exhibits high interannual variability, with the majority of annual rainfall condensed into three months (Jan - Mar). Species in this region are predominantly deciduous, with over 90 % of individuals' leaves falling during the dry season (ALA Lima unpubl. res.). According to the Köppen system the climate is BSwh', *i.e.* warm and dry with the rainy season occurring in the summer months. The annual rainfall is ca. 653 mm, with a mean temperature of 23.8 ± 0.92 ºC (Silva & Almeida 2013). The annual evapotranspiration of 2000 mm far exceeds annual rainfall (Sampaio 1995). Inside the nature reserve, soils are mainly of three classes: Litholic soils, Neossol soils and Cambisol soils (Silva & Almeida 2013).

Data collection

We collected diaspores of woody species from July 2009 to July 2011, and obtained phenological information on northeast dry forests from the literature (Griz & Machado 2001; Lima & Rodal 2010). Woody species were defined based on a previously phytosociological survey in this study area (Farias *et al*. 2016). Diaspores were manually collected, packed in plastic bags and taken to the laboratory, where seeds were then removed and germinated immediately. Twenty seeds from each species were planted in trays containing a mixture of sand and organic compost at a ratio of 1:1. The samples were maintained under the ambient conditions and were watered daily. We monitored all seedlings until they had at least one pair of protophilus (first true leaves); we then collected and dried them in a drying oven.

Next, we classified the seedlings into morphological and functional groups following Garwood (1996). This classification used ecologically important cotyledon features, such as exposure (phanerocotylar or cryptocotylar), position (epigeal or hypogeal) and function (foliaceous or reserve storage) to determine five functional groups of seedlings: phanerocotylar epigeal with foliaceous cotyledons (PEF), phanerocotylar epigeal with reserve storage cotyledons (PER), phanerocotylar hypogeal with reserve storage cotyledons (PHR), cryptocotylar hypogeal with reserve storage cotyledons (CHR) and cryptocotylar epigeal with reserve storage cotyledons (CER).

Additionally, we classified plant species according to their dispersion mode as autochoric; anemochoric and zoochoric (Pijl 1982). The seed size was divided into four size classes: < 0.5 cm; 0.5 – 1.0 cm; 1.1 – 2.0 cm; > 2 cm (adapted from Miquel 1987). Ecological traits related to ecological strategies for dealing with seasonal environmental conditions were obtained from previous studies performed in the same study area. Maximum height was obtained from Farias *et al*. (2016), while leaf lifespan, wood density and water potential in the dry season were obtained from Lima *et al*. (2012).

Data analysis

We used an Analysis of Similarity (ANOSIM) to test if the functional groups of seedlings were related to life history traits (seed size, habit and dispersion mode) of species and used a Nonlinear Multidimensional Scaling (NMDS) ordination based on 1000 permutations to visualise these relationships. We also conducted a Principal Component Analysis (PCA) to evaluate if seedling functional groups are related to plant traits (water potential, wood density, leaf lifespan and maximum height) which reflect ecological responses to environmental conditions. Plant trait values were log10-transformed to standardise and to normalise these variables. Additionally, we used linear regression to test whether the spectrum of seedling groups varied with rainfall conditions (a component of environmental filtering) comparing the frequency of seedlings' functional groups recorded in different forests with the annual rainfall range. All analyses were performed using R software (R Development Core Team 2016).

Results

Seedlings from 26 species belonging to 24 genera and ten families were recorded (Tab.1). This value represents 53 % of the number of woody species registered in the Caatinga vegetation of the Mata da Pimenteira State Park. The families with the highest number of species were Fabaceae (eight), Euphorbiaceae (four) and Malvaceae (three), which are the most representative families in the Caatinga ecosystem (Moro *et al*. 2014). PEF seedlings were the most prevalent functional group, recorded for 52 % of species, followed by 24 % PER seedlings and 16 % PHR seedlings from total number of species. CHR seedlings showed the lowest proportion, representing only 8 % of the woody seedlings studied. Among the five possible functional groups likely to occur, CER was the only group not registered.

We found no grouping in relation to functional groups of seedlings and species life cycle traits, such as seed size, habit and dispersal mode ($R = 0.01$, $p = 0.42$, Fig. 1). However, the functional classification of seedlings was related to the range of strategies exhibited by plant species to deal with stressful environmental conditions, where PEF seedlings showed the highest range of variation, followed by PER and PHR seedlings, respectively (Fig. 2). The first three axes of the PCA analysis explained 91.1 % of data variation. The first axis explained 43.0 % while the second and third explained 26.4 % and 21.7 %, respectively. The water potential in the dry season and the wood density traits were correlated with the first axis, the leaf lifespan with the second axis and the maximum height with the third axis.

The frequency of functional groups of seedlings varied in function of annual rainfall ($R^2 = 0.77$, $F = 10.59$, $p < 0.04$, Tab. 2). The frequency of PER seedlings increased rainfall decreased, whereas CHR seedlings showed the opposite tendency.

Discussion

We investigated the relationship between functional groups of seedlings – which are assumed to reflect strategies associated with seedling establishment – and species' life history and plant functional traits associated with seasonal ecosystems. We found no pattern between functional groups of seedlings and plants' life history traits. The absence of a relationship, especially between functional groups and seed size, may be due to the low frequency of CHR seedlings in the Caatinga vegetation. This functional group

Table 1. Functional groups of 26 species of woody plants from Caatinga vegetation at Mata da Pimenteira State Park, Brazil. Followed by functional group: PEF – Phanerocotylar Epigeal Foliaceous; PER - Phanerocotylar Epigeal with Reserve; PHR - Phanerocotylar Hypogeal with Reserve, CHR – Cryptocotylar Hypogeal with Reserve; Seed size (1: <0,5cm; 2: 0,5-1,0cm; 3: 1-2cm; 4: >2cm.); Dispersal mode (ane – anemochoric; auto – autochorous; zoo - zoochorous) and Habit (T: tree; S: shrub) of each species.

Family/Specie	Functional group	Seed size	Dispersal mode	Habit
Anacardiaceae				
Myracrodruon urundeuva Allemão	PEF	1	Ane	T
Schinopsis brasiliensis Engler	PEF	3	Ane	T
Spondias tuberosa Arruda	PER	4	Zoo	T
Annonaceae				
Annona leptopetala R. E. Fr.	PEF	2	Zoo	T
Apocynaceae				
Aspidosperma cuspa SFBlake ex Pittier	CHR	3	Ane	T
Aspidosperma pyrifolium Mart.	PEF	4	Ane	T
Burseraceae				
Commiphora leptophloeos (Mart.) J. B. Gillet	PER	3	Zoo	T
Capparaceae				
Cynophalla flexuosa (L.) J. Presl	CHR	2	Zoo	S
Euphorbiaceae				
Croton rhamnifolioides Pax & K. Hoffm.	PEF	1	Auto	S
Ditaxis desertorum Pax & K. Hoffm.	PEF	1	Auto	S
Sapium glandulosum (L.) Morong	PEF	2	Zoo	T
Sebastiania macrocarpa Mull. Arg.	PEF	1	Auto	T
Fabaceae				
Amburana cearesis (Allemão) A. C. Smith	PHR	4	Ane	T
Anadenanthera colubrina (Vell.) Brenan	PHR	3	Auto	T
Bauhinia cheilantha (Bong.) Steud.	PHR	1	Auto	S
Libidibia ferrea (Mart. ex Tul.) L. P. Queiroz	PER	3	Zoo	T
Mimosa tenuiflora Poir.	PHR	1	Ane	T
Parapiptadenia zehntneri (Harms) M. P. Lima & H. C. Lima	PER	3	Ane	T
Piptadenia stipulacea (Benth.) Ducke	PER	2	Auto	T
Poincianella pyramidalis (Tul.) L. P. Queiroz	PER	3	Auto	T
Malvaceae				
Ceiba glaziovii (Kuntze) k. Schum.	PEF	2	Ane	T
Helicteres baruensis Jacq.	PEF	1	Auto	S
Pseudobombax marginatum (A. St.-Hil. A. Juss & Cambess.) A. Robyns	PEF	2	Ane	T
Rhamnaceae				
Ziziphus joazeiro Mart.	PEF	3	Zoo	T
Rubiaceae				
Guettarda angelica Mart. ex Müll.Arg.	PEF	1	Zoo	S

usually exhibits large seeds, with large reserves and slow development associated with the high capacity to survive in competitive environments, and thus these seedlings are less likely to be successful in the presence of strong abiotic restrictions such as those found in this semi-arid region.

In contrast, seedling functional groups were related to a range of plant functional traits that express ecological strategies to cope with drought conditions. Seedlings with protected cotyledon and reserve storage had a smaller range of values of traits related to ecological strategies, which indicates that these species are more similar in their environmental requirements and abilities to deal with variation in abiotic conditions. Instead, species that have exposed cotyledons during germination presented a broad variation of traits, which are represented by species with quick development, fast colonisation and growth rates. Such strategies are likely to be an important factor in dealing with a short growing season as experienced by plant species in seasonally dry tropical forests.

PEF and PER seedlings were the most frequent, differing from other Neotropical forests (Ibarra-Manríquez 2001) where CHR seedlings represent a high proportion of species together with PEF, which always display the highest frequency. It is likely that this difference is due to differences in rainfall regimes, which can impose strong environmental filtering in the case of seasonal environments such as the Caatinga ecosystem. For instance, CHR seedlings are exceptionally frequent in forests with annual rainfall greater than 1500 mm (Garwood 1996) where habitat conditions confer an advantage to species with high competitive capacities. In contrast, we found that PEF and PER seedlings were the most successful at coping with broad differences in water availability,

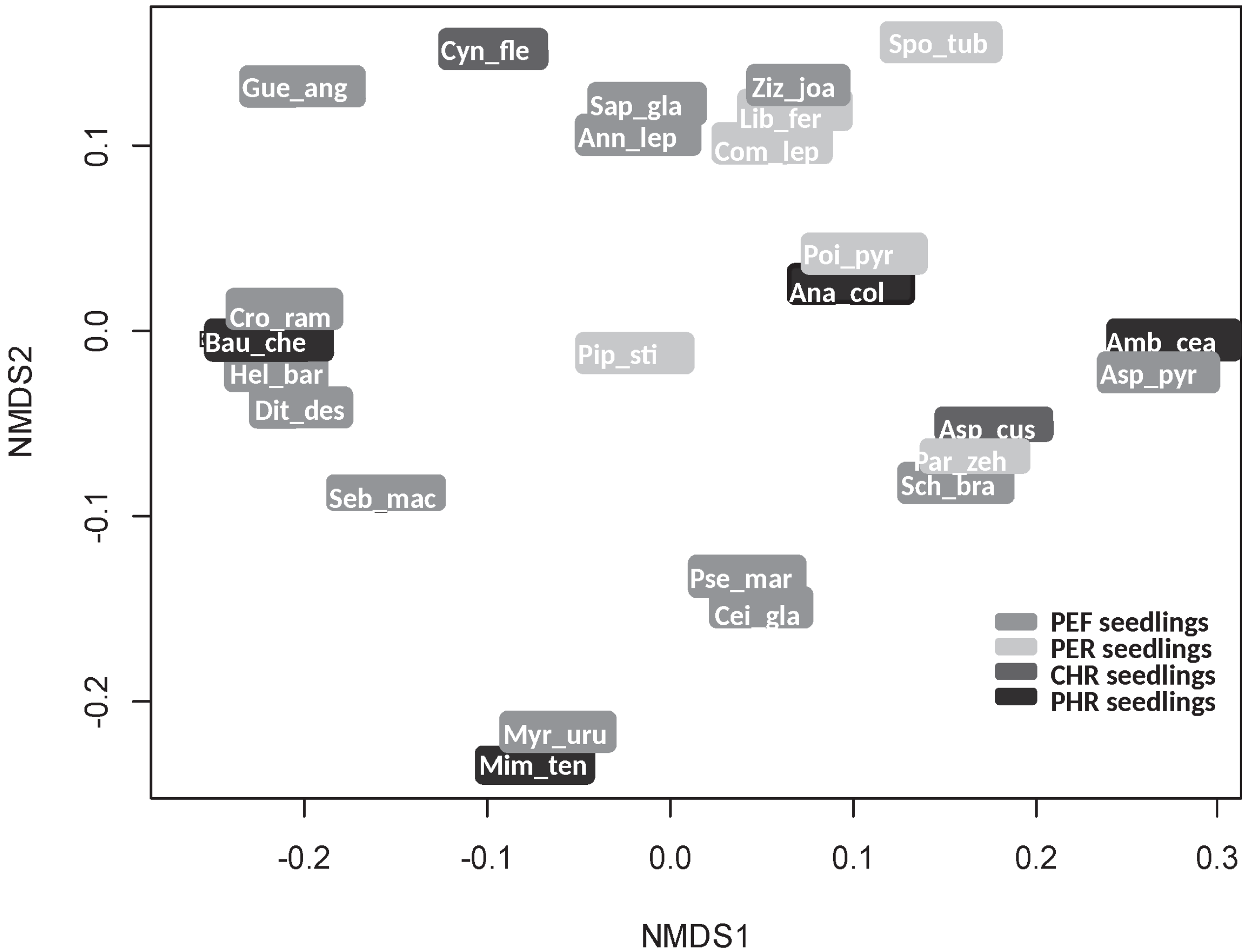

Figure 1. Non-metric multidimensional scaling (NMDS) based on life history traits (seed size, dispersal mode and habit) showing the relationships between functional groups of seedlings among woody species recorded in the Mata da Pimenteira State Park, NE Brazil. Functional groups: PEF – Phanerocotylar Epigeal Foliaceous; PER – Phanerocotylar Epigeal with Reserve; PHR - Phanerocotylar Hypogeal with Reserve; CHR – Cryptocotylar Hypogeal with Reserve. Species: Amb_cea = *Amburana cearesis*, Ana_col = *Anadenanthera colubrina*, Ann_lep = *Annona leptopetala*, Asp_pyr = *Aspidosperma pyrifolium,* Bau_che = *Bauhinia cheilantha*, Com_lep = *Commiphora leptophloeos*, Cro_rha = *Croton rhamnifolioides*, Cyn_fle = *Cynophalla flexuosa*, Myr_uru = *Myracrodruon urundeuva*, Pip_sti = *Piptadenia stipulacea,* Poi_pyr = *Poincianella pyramidalis*, Pse_mar = *Pseudobombax marginatum*, Sap_gla = *Sapium glandulosum*, Seb_mac = *Sebastiania macrocarpa*, Spo_tub = *Spondias tuberosa*, Ziz_joa = *Ziziphus joazeiro*.

which may represent an important adaptive strategy for seasonally dry tropical forests.

Although this classification based on cotyledon types resulted in a categorical division of functional groups, the distinction between photosynthetic and storage cotyledons is not completely dichotomous, except for cryptogeal species, where the cotyledons are for storage only (Kidson & Westoby 2000). For phanerocotylar epigeal species - those in which the cotyledons are exposed and located above the ground, as occurs in PEF and PER seedlings – storage and photosynthetic functions showed a continuous across species (Kidson & Westoby 2000). It is likely that this is related to a broad range of strategies and niches, manifested by these groups as traits related to survival and be successful in varied conditions of the semi-arid region, as highlighted in PCA analysis.

Our analysis of seedling functional profile across sites with different average rainfalls showed an increase in PHR seedling with decreasing rainfall, while CHR seedlings showed the opposite tendency. It seems that the phanerocotylar strategy is an interesting mechanism by which such seedlings are exposed to the brief favourable environmental conditions in which their cotyledon can support an additional role in photosynthesis. In fact, Fabaceae, Euphorbiaceae and Malvaceae, the most common families recorded here and in the Caatinga ecosystem as a whole (Moro *et al.* 2014), only presented species with phanerocotylar seedlings. Functional groups of seedlings were generally conserved within these families. Both Malvaceae and Euphorbiaceae exhibited only PEF seedlings, which suggests that species of these families are good initial

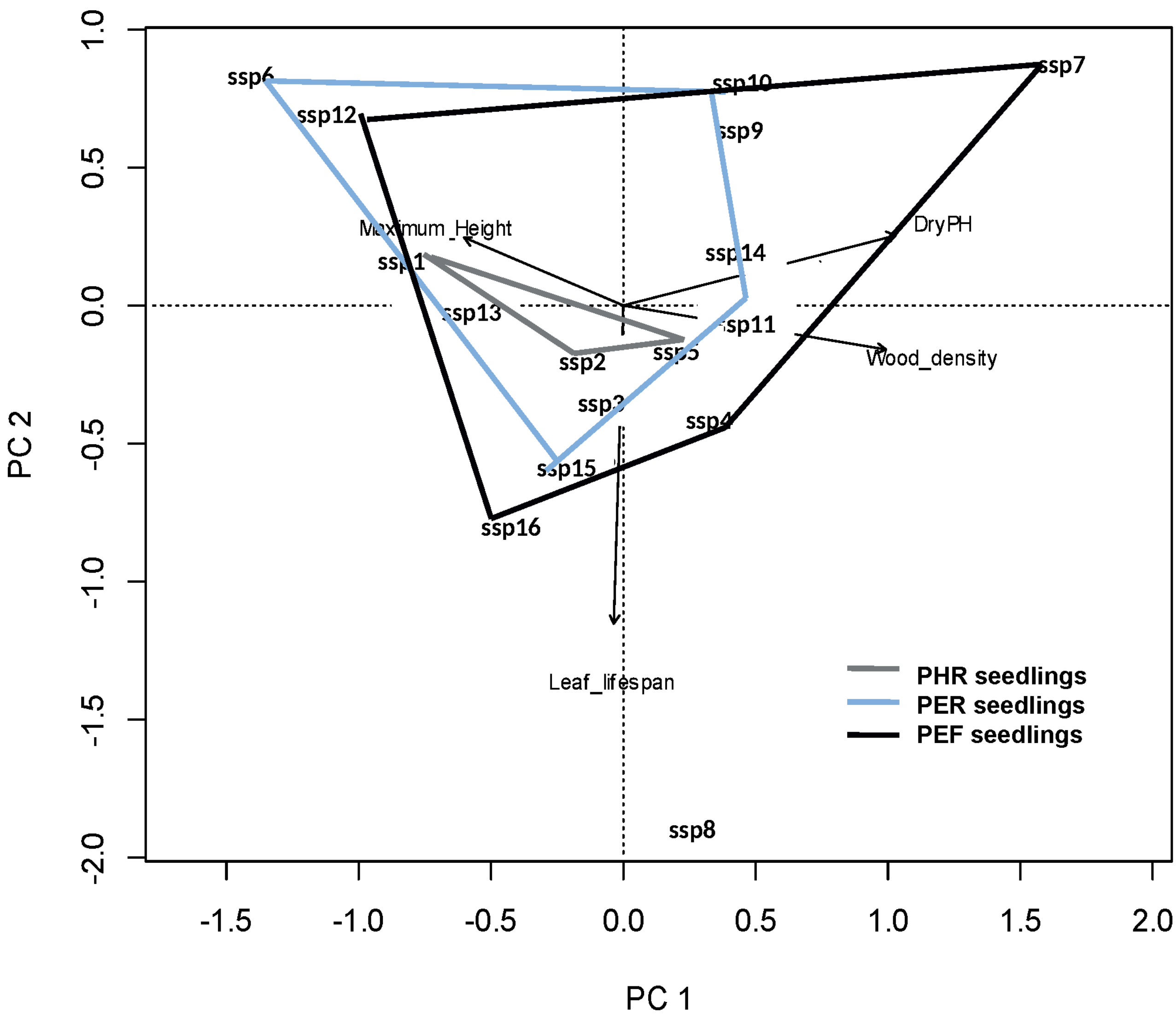

Figure 2. Principal Component Analysis showing plant species recorded in the Mata da Pimenteira State Park, NE Brazil, and their association with seed size, maximum height, leaf lifespan, wood density and water potential in the dry season and seedling functional groups. Functional groups: PEF – Phanerocotylar Epigeal Foliaceous; PER – Phanerocotylar Epigeal with Reserve; PHR - Phanerocotylar Hypogeal with Reserve. Plant Species: ssp1 = *Amburana cearesis*, ssp2 = *Anadenanthera colubrina*, ssp3 = *Annona leptopetala*, ssp4 = *Aspidosperma pyrifolium,* ssp5 = *Bauhinia cheilantha*, ssp6 = *Commiphora leptophloeos*, ssp7 = *Croton rhamnifolioides*, ssp8 = *Cynophalla flexuosa*, ssp9 = *Myracrodruon urundeuva*, ssp10 = *Piptadenia stipulacea,* ssp11 = *Poincianella pyramidalis*, ssp12 = *Pseudobombax marginatum*, ssp13 = *Sapium glandulosum*, ssp14 = *Sebastiania macrocarpa*, ssp15 = *Spondias tuberosa*, ssp16 = *Ziziphus joazeiro*.

Table 2. Percentage of morphofunctional groups between forest types according to rainfall (modified Ibarra-Manríquez 2001 increased by Ressel 2004 and this study). PEF – Phanerocotylar Epigeal Foliaceous; PHR - Phanerocotylar Hypogeal with Reserve; PER – Phanerocotylar Epigeal with Reserve; CHR – Cryptocotylar Hypogeal with Reserve; CER – Cryptocotylar Epigeal with Reserve; *N* - number of seedlings recorded in the representative value 50 to 75 % of the total woody flora in the site.

Site	Vegetation	PEF	PHR	PER	CHR	CER	*N*	Rainfall (mm)
Brazil	Dry Forest	52	16	24	8	-	25	800
Brazil	Dry Forest	51	8	17	23	1	122	1650
Gabon	Rain Forest	39	9	24.8	21.9	5.2	210	1760
Panama	Rain Forest	42.9	8.8	16.1	28.8	3.4	205	2600
Mexico	Rain Forest	49.5	7.2	9.5	31.40	2.4	210	4560

colonizers and opportunists, as they grow rapidly during the rainy season. Fabaceae, which is the most diverse family in dry forests (Gentry 1995; Moro *et al*. 2014; Vargas *et al*. 2015), showed PHR and PER seedlings in equal proportion. The fact that all species of this family have seedlings with reserves indicates a certain level of tolerance to highly varied and unpredictable climatic conditions, which is evidence of why this lineage is so successful in seasonally dry environments. Moreover, phanerocotyledons vary their position at several levels, conferring different strategies to species of this family, which may help Fabaceae species to occupy different niches in such environment.

Our findings provide broader knowledge regarding functional groups of seedlings, showing that the variation in frequency of these groups depends on annual water availability, which can reflect the role of environmental filtering as an important driver of assembly rules in seasonally dry tropical forests. Also, the most frequent functional groups exhibited a broad variation in plant traits, indicating that such groups could be related to survival in seasonally marked conditions such as those found in the Caatinga ecosystem. Future studies should focus on how these functional groups response to intra and inter-annual variation of rainfall in seasonally dry tropical forests to address the effects of seasonality driving changes at population and community levels. Furthermore, research efforts should be devoted to the dynamics of change in these strategies along gradients of seasonality and rainfall within the Caatinga ecosystem, which may assist in predicting plant species behaviour with regard to ongoing climate change.

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