

## Ecological grouping of tropical trees in an evergreen forest of the Sierra del Rosario, Cuba\*

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**ABSTRACT.** The ecological grouping of 32 species of tropical trees was determined using quantitative (15) and qualitative (5) traits of the regeneration phase. Three large groups or strategies of establishment were identified by means of a principal component analysis. Seed dry mass was the trait that contributed most to the formation of these groups and to the ecological variation among species. The first group comprised pioneer species and non-pioneers established in open sites, having small seeds with scarce seed reserves, high seedling growth rates and high phenotypic plasticity when grown in substrates with varying availability of nutrients. In opposite position to this group, there was another grouping which includes climax or mature forest species, having large seeds with abundant reserves, low growth rates and scarce phenotypic plasticity. Lastly, a third group occupying an intermediate position in the forest succession continuum was identified; these species showed regeneration traits that facilitate the colonization of many microsites. On the other hand, the dispersal mode, collection time and presence of seed dormancy were not helpful variables for species classification; whereas dormancy and seedling type were adequate for separating succession groups. It is suggested that the different position of every species in each ecological functioning group and along the axes of principal components indicates that each species has a specific response that contributes to coexistence by reducing inter-specific competition.

**KEY WORDS.** Forest succession, growth analysis, phenotypic plasticity, seed dormancy, seed size.

### INTRODUCTION

Many mechanisms contribute to the maintenance of tree diversity in tropical forests. Some of these have focused on niche differentiation or resource partitioning during the regeneration phase (Grubb, 1977), and include differences in seed germination responses to environmental variation (Muñoz *et al.*, 2001; Daws *et al.*, 2002; Pearson *et al.*, 2002; Sánchez *et al.*, 2003) and differential seedling responses to a heterogeneous light environment (Metcalf and Grubb, 1997; Dalling *et al.*, 2004). Although considerable attention has been given to seedling responses to irradiance, these alone are not sufficient to explain species coexistence, since most tropical tree species are shade-tolerant and exhibit little evidence of partitioning of the light environment (Bloor and Grubb, 2003). However, the role of other potential differences among species remains insufficiently examined.

Variation in soil fertility is another additional source of heterogeneity in tropical forests (Burslem *et al.*, 1996); therefore, nutrient availability in soils could also affect the distribution and abundance of tree species. It is well known that plants having scarce food reserves in their seeds establish themselves better in clearings of disturbed sites (Bullock, 2000; Bloor and Grubb, 2003); whereas the species that have large seed food resources tend to establish in shaded sites or nutrient-poor soils (Bullock, 2000; Westoby *et al.*, 2002). This mechanism of niche differentiation, related to nutrient availability, has been well determined in temperate and arid environment species (Fenner, 1983; Jurado and Westoby, 1992; Milberg *et al.*, 1998); but is little if at all studied in neotropical tree species (Kitajima, 2002; Sánchez *et al.*, 2007).

In the other hand, the transition from seed to seedling is a high-risk stage in plant life-cycle (Harper, 1977). Consequently, mechanisms that minimize the risk to this transition will be

under strong selection pressure (Meyer *et al.*, 1997), and natural selection should favour seed germination patterns that increase the probability of successful seedling establishment (Daws *et al.*, 2002; Baskin and Baskin, 2004).

According to all these data, it is not strange that traits related to the regeneration phase had been used frequently for defining ecological functioning groups or establishment strategies of tropical trees. Several workers have stated that tropical trees can not be placed in similar ecological groups of species without a previous knowledge of their seed and seedling ecology (Swaine and Whitmore, 1988; Martínez-Ramos *et al.*, 1989; Whitmore, 1989). Therefore, the ecological classification of tropical trees proposed by Swaine and Whitmore (1988), which is the most widely used in the tropics, is based upon the concept of regeneration niche (Grubb, 1977). Swaine and Whitmore (1988) have established that tropical forest trees can only be grouped in two ecological categories: pioneers and climax (non-pioneers) species and they believe that pioneers can only germinate and establish in clearings, whereas climax species generally germinate and establish in shaded sites or under the forest canopy.

However, other workers (Bazzaz, 1996; Herrera *et al.*, 1997; Bullock, 2000) have claimed that this classification does not correspond to the high diversity neither to the complex of competition stages of substitution and stabilization found in tropical forests. They also remark that pioneers and climax are the opposite extremes in a wide succession gradient, which represents all the possible responses to environmental perturbations. Therefore, the forest succession continuum can not possibly rely on just two succession or establishment groups.

In Cuba, the existence of a succession continuum (i.e., continuum *r-K*) was initially proposed by Herrera *et al.* (1997) for several succession stages in dry-saline and humid forests

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and based upon morphological seed traits and physiological characteristics of advanced stages of plant development. Muñoz (1998), Muñoz *et al.* (2001) and Sánchez *et al.* (2003) proposed the existence of the continuum *r-K* in the pioneer tree group considering morph-physiological seed traits only. However, it has never been determined how the establishment strategies of tree species are grouped, using only seed and seedling traits. Therefore, in this paper the usefulness of these regeneration traits for the ecological grouping of 32 tree species in a tropical evergreen forest in the Sierra del Rosario Biosphere Reserve (SRBR), Cuba is assessed.

## MATERIALS AND METHODS

**Site description and species selection.** The SRBR is located in the easternmost part of Sierra del Rosario, Pinar del Río, Cuba (22° 45' N, 82° 50' W) and has an extension of 25000 ha. The flora, vegetation and geology of SRBR are described in greater detail elsewhere by Herrera *et al.* (1988a). In the region, annual average air temperature is 24.4°C. Lowest and highest mean values understorey soil temperature at 2 cm depth during summer (May-October) are 22.3°C and 24.5°C, respectively; whereas in clearing (i.e., large canopy gap) they are 22.5°C and 34.5°C (Vilamajó *et al.*, 1988). On SRBR, the total annual

precipitations is ca. 2300 mm, rainfall in lowest in December, January, February and March, begin to increase in April, reaches the maximum in July, decreases from October to November and finally reaches the minimum in December (Vilamajó *et al.*, 1988). Based on these data and following the approach proposed by Sautu *et al.* (2006), we recognized three seasons in this study: dry season, December-March; early rainy season, April-July; and late rainy season, August-November.

The plants selected for this study are common gap-demanding or understorey component of primary forest flora of the SRBR (Table 1) (Herrera *et al.*, 1997). Only *Albizia lebeck* is a species naturalized in the SRBR, as occurred in different forests from Cuban Archipelago. The tree species were chose on the basic of their frequency at the study site and the availability of seeds. The great majority of the plant studies have been used in the Cuban timber industry (Betancourt, 1987) and all they are proposed for plans of tropical afforestation (Herrera *et al.*, 1997). For each of the 32 species, author, common name (in Spanish), family, diaspore type, dispersal mode, dispersal time, seedling type and dormancy class are present in Table 1. Family names follow Angiosperm Phylogeny Group (1998). Generic names are used for all species, except for *Calophyllum brasiliense* and *Calophyllum pinetorum*.

Table 1. Scientific name (including author), common name (in Spanish), family and life-history characteristics for the 32 tropical tree species studied from the SRBR. Dispersal modes follow van der Pijl (1982): AN, anemochory; AU, autochory; ZOO, Zoochory; BA, barochory. Early seedling morphology after Garwood (1996): PEF, phanerocotylar-epigeal-foliaceous; PER, phanerocotylar-epigeal-reserve; CHR, cryptocotylar-hypogeal-reserve; CER, cryptocotylar-epigeal-reserve. Classes of seed dormancy after Baskin and Baskin (2004): ND, non dormant; PY, physical dormancy; PD, physiological dormancy. Based on annual rainfall data, it recognized three season of dispersal/collection: Dry season (DS), December-March; early rainy season (ERS), April-July; late rainy season (LRS), August-November.

| Tree species                                | Common name      | Family         | Dispersal mode | Diaspore type | Dispersal time | Seedling type | Dormancy class |
|---|------------------|----------------|----------------|---------------|----------------|---------------|----------------|
| <i>Albizia lebeck</i> (L.) Benth            | Aroma francesa   | Fabaceae       | AU             | Seed          | LRS            | PER           | PY             |
| <i>Alchornea latifolia</i> Sw.              | Aguacatillo      | Euphorbiaceae  | ZOO            | Seed          | ERS            | PEF           | PD             |
| <i>Allophylus cominia</i> (L.) Sw.          | Palo de caja     | Sapindaceae    | ZOO            | Fruit         | DS             | PEF           | PD             |
| <i>Andira inermis</i> (W. Wright) Kunth     | Yaba             | Fabaceae       | ZOO            | Fruit         | DS             | CHR           | PD             |
| <i>Bauhinia purpurea</i> Benth              | Pata de vaca     | Fabaceae       | AU             | Seed          | ERS            | PER           | ND             |
| <i>Caesalpinia violacea</i> (Mill.) Standl. | Yarúa            | Fabaceae       | AU             | Fruit         | LRS            | PER           | ND             |
| <i>Calophyllum brasiliense</i> Cambess      | Ocuje            | Clusiaceae     | ZOO, BA        | Fruit         | LRS            | CHR           | PD             |
| <i>Calophyllum pinetorum</i> Bisse          | Ocuje            | Clusiaceae     | ZOO, BA        | Fruit         | DS             | CHR           | PD             |
| <i>Cecropia schreberiana</i> Miq.           | Yagruma          | Cecropiaceae   | ZOO            | Fruit         | ERS            | PEF           | ND             |
| <i>Ceiba pentandra</i> (L.) Gaertn.         | Ceiba            | Malvaceae      | AN             | Seed          | ERS            | PEF           | PD             |
| <i>Chrysophyllum oliviforme</i> L.          | Caimitillo       | Sapotaceae     | ZOO            | Fruit         | ERS            | PER           | ND             |
| <i>Colubrina arborescens</i> (Mill.) Sarg.  | Bijaguara        | Rhamnaceae     | AU             | Seed          | DS             | PEF           | PD             |
| <i>Cordia collococca</i> L.                 | Ateje            | Boraginaceae   | ZOO            | Fruit         | ERS            | PEF           | PD             |
| <i>Cupania americana</i> L.                 | Guara común      | Sapindaceae    | ZOO, BA        | Seed          | ERS            | CHR           | PD             |
| <i>Ehretia tinifolia</i> L.                 | Roble prieto     | Boraginaceae   | ZOO            | Fruit         | LRS            | PEF           | PD             |
| <i>Ficus maxima</i> P. Mill                 | Jagüey macho     | Moraceae       | ZOO            | Fruit         | ERS            | PEF           | ND             |
| <i>Gliricidia sepium</i> (Jacq.) Steud      | Piñón florido    | Fabaceae       | AU             | Seed          | ERS            | PER           | ND             |
| <i>Guazuma ulmifolia</i> Lam.               | Guásima          | Malvaceae      | ZOO, BA        | Fruit         | DS             | PEF           | PY             |
| <i>Lysiloma latisiliquum</i> Benth          | Sabicú           | Fabaceae       | BA             | Fruit         | LRS            | PER           | PY             |
| <i>Matayba apetala</i> (Macf) Radlk.        | Macurije         | Sapindaceae    | ZOO            | Seed          | ERS            | CHR           | PD             |
| <i>Muntingia calabura</i> L.                | Capulí           | Elaeocarpaceae | ZOO            | Fruit         | ERS            | PEF           | ND             |
| <i>Ocotea leucoxyloides</i> (Sw.) Mez       | Aguacatillo      | Lauraceae      | BA             | Fruit         | ERS            | CHR           | PD             |
| <i>Poeppigia procera</i> C. Presl.          | Tengue           | Fabaceae       | BA             | Seed          | DS             | PER           | ND             |
| <i>Prunus occidentalis</i> Sw.              | Cuajani          | Rosaceae       | ZOO, BA        | Fruit         | ERS            | PER           | PD             |
| <i>Pseudolmedia spuria</i> (Sw.) Griseb.    | Macagüa          | Moraceae       | ZOO            | Fruit         | ERS            | CHR           | PD             |
| <i>Psychotria grandis</i> Sw.               | Tapa camino      | Rubiaceae      | ZOO            | Fruit         | LRS            | PEF           | PD             |
| <i>Samanea saman</i> (Jacq.) Merrill        | Algarrobo        | Fabaceae       | BA             | Fruit         | ERS            | PER           | ND             |
| <i>Sideroxylon foetidissimum</i> Jacq.      | Jocuma           | Sapotaceae     | ZOO            | Fruit         | DS             | CER           | PD             |
| <i>Talipariti elatum</i> (Sw.) Fryxell      | Majagua azul     | Malvaceae      | BA             | Seed          | DS             | PEF           | PY, PD         |
| <i>Trema micrantha</i> (L.) Blume           | Capulí cimarrón  | Ulmaceae       | ZOO            | Fruit         | LRS            | PEF           | ND             |
| <i>Trichilia hirta</i> L.                   | Cabo de hacha    | Meliaceae      | BA             | Seed          | ERS            | CHR           | ND             |
| <i>Trichospermum mexicanum</i> (DC.) Baill  | Majaguilla macho | Malvaceae      | AN             | Seed          | ERS            | PEF           | ND             |

The fresh seeds were collected in the Ecological Station “El Salón” (central section of the SRBR), covered by to submontane seasonal evergreen forest (i.e., moist tropical forest), with a closed canopy 30 m tall, where are distinguished emergent, dominant and dominated trees, and with 13% of trees that lose their leaves during the months of smaller rainfall. The endemism in collection site is poor (11%). One of the 32 study species is endemic (*Calophyllum pinetorum*). Throughout this paper, “seed” means a true seed or a diaspore (true seed + endocarp). Species whose diaspores included endocarp of camara was *Andira* and drupes were *Allophylus*, *Cordia*, *Ehretia*, *Prunus*, *Pseudolmedia* and *Trema*.

**Brief description of the experiments used in data gathering.** Tests were performed under laboratory and nursery conditions (from 2003 to 2006) and sponsored by a research project, the main goal of which was the determination of the role of seed dormancy and size in the establishment of tropical trees (Sánchez *et al.*, 2007).

Germination studies were done in temperature and light controlled incubators. To simulate the variations that suffer the soil temperature and light from the inside forest until a clearing a factorial experiment was planned. Four temperatures and two light conditions were used, for a total of eight treatments for species. Germination responses were obtained at a constant temperature of 25°C and at alternating temperature regimes of 25/30°C, 25/35°C and 25/40°C. The light treatments were: light exposure and constant darkness. The system of classification of

seed dormancy from Baskin and Baskin (2004) was employed.

Our conditions in the nursery were similar to those in commercial production nurseries in Cuba, i.e., ambient temperature (23-30°C) and under natural light (30-40% full sunlight). Seedlings were planted out individually in white plastic pots contained coarse river sand (nutrient-very poor) or two soil types from the natural site of distribution of the species in the SRBR. The forest soils were Eutric-Mollic Cambisol and Calcari-Mollic Cambisol having medium and high natural fertility (Driessen *et al.*, 2001). These differed in their texture, nutrient content and arbuscular mycorrhizae (see Sánchez *et al.*, 2007). Seedlings were harvested 28 days after planting by immersion each pot in water and after rising roots carefully with water to remove sand or soil. At harvest, all seedlings had at least two leaves in addition to the cotyledons. Leaves, stems and roots were separated, dried at 70°C for 48 hr and weighted. Based on the harvest data, a number of seedling traits were calculated.

**Variables and analysis for identifying ecological groups.**

In the study of Sánchez *et al.* (2007), 36 quantitative variables related to the regeneration niche of the species under study were determined. However, only 15 quantitative variables were used in this paper, mainly those that turned out to be highly significant among species and aiming at deleting redundant and low-contributing characters. A brief description of these variables is given in Table 2.

Table 2. Description of the variables used for the identification of the groups of ecological function.

| Variables                                    | Abbreviation/units | Description   | Source  |
|--|--------------------|---|---|
| Seed dry mass                                | SDM (mg)           | Mean dry mass of seeds was determined individually in 100 seeds or in five replicas (50 seeds each), in accordance to seed size/species. Seeds were dried at $103 \pm 2^\circ\text{C}$ for 17 hr and weighted after drying. When seed mass was determined, any fleshy part of fruit wall was removed, as also any aril or sarcotesta.   | ISTA (1999)   |
| Seed reserve dry mass                        | SRM (mg)           | This variable represented mean dry mass of the embryo plus endosperm (if present). Sample size and drying were determined in a similar way to that described in SDM.  | ISTA (1999)   |
| Seed moisture content                        | SMC (%)            | The initial water contents of seeds based on fresh mass was determined immediately after recollection of fruits/seeds. Sample size and seed treatments were similar to those described in SDM.  | ISTA (1999)   |
| Percentage of seed dry mass in coat          | PSC (%)            | To calculate the allocation to defence in seed, the fraction of the mass of covering structures (testa, plus endocarp if present) to the mass of the total dispersal unit was determined. The sample size and drying went similar to those described for the SDM.   | Sánchez <i>et al.</i> (1997), Daws <i>et al.</i> (2005) |
| Percentage of seed dry mass in reserve       | PSR (%)            | To calculate the allocation to reserve in seed, the fraction of the mass of reserves (embryo, plus endosperm if present) to the mass of the total dispersal unit was determined. The sample size and drying went similar to those described for the SDM.  | Fenner (1983), Sánchez <i>et al.</i> (1997)             |
| Relative light germination index             | RLG                | The germination percentage in light and darkness were used to calculate an index expressing a light requirement: Relative light germination (RLG). This index was calculated according to: $RLG = GL/(Gd + GL)$ , where GL = the germination percentage in light, and Gd = the germination percentage in darkness. RLG represents a range of values varying from 0 (germination only in darkness) to 1 (germination only in light). The germination values used to calculate the RLG come from the optimal temperature of germination for each species. | Milberg <i>et al.</i> (2000)                            |
| Range of optimal temperature for germination | ROT                | Temperature range in which the highest percentage of final germination under white light was reached.   | Sánchez <i>et al.</i> (2007)                            |

Table 2. Continued. Description of the variables used for the identification of the groups of ecological function.

| Variables                       | Abbreviation/<br>units   | Description  | Source                          |
|---------------------------------|--------------------------|--|---------------------------------|
| Coefficient of germination rate | CGR (%)                  | The CGR was calculated for each replicate by dividing the final number of seeds that germinated ( $N$ ) by the number of germinated seeds on the particular day on which a count was made ( $n_i$ ) multiplied by the number of days from the start of experiment ( $d_i$ ) and summing for all day on which germination occurred: $CGR = N / \sum n_i d_i \times 100$ . All values of CGR are between 0 (no germination) and 100 (fastest germination rate).  | Alm <i>et al.</i> (1993)        |
| Germination begin               | GB (day)                 | Day of germination start under optimal temperature range for germination.  | Sánchez <i>et al.</i> (2007)    |
| Variance of seed dimensions     | VSD                      | For each species, 100 seeds (dispersal units) were weight and the shape of seeds was captured by measuring length, width and depth of a seed (with a vernier caliper) and dividing all values through length so that length is unity, and then calculating the variance of these three values by dividing the summed squared deviation from the mean by $n - 3$ : $(\sum(x - \bar{x})^2) / n$ . Thus, perfectly spherical seed have a variance value of 0 and elongated or flattened seeds have variances of up to 0.33. | Thompson <i>et al.</i> (1993)   |
| Seed longevity                  | SL (month)               | Seed longevity was number of the months that seeds remained viable (total germination > 5%) stored at 25°C and 60% relative humidity in paper bags.  | Sánchez <i>et al.</i> (2007)    |
| Total seedling dry mass         | TSM (mg)                 | Mean value of total dry mass of seedlings (excluding thick cotyledons) which grew in nutrient-poor substrate during 28 days after germination.   | Sánchez <i>et al.</i> (2007)    |
| Relative growth rate            | RGR (day <sup>-1</sup> ) | Relative growth rate was calculated according to: $RGR = (\ln W - \ln S) / t$ , where $W$ = average dry mass of seedling including cotyledons at harvest; $S$ = average dry mass of seed reserve; $t$ = number of day after germination (28 days). This index represents the growth rate of seedlings grown in nutrient-very poor substrate. Therefore, the increase in growth rate depended almost exclusively on seed reserves.  | Milberg <i>et al.</i> (1998)    |
| Lateral root mass fraction      | LRMF (mg/mg)             | Production of lateral roots was determined in seedlings grown in nutrient-very poor substrate. This variable represented the relation between dry mass of lateral roots/dry mass of total roots.   | Burslem <i>et al.</i> (1996)    |
| Mean phenotypic plasticity      | MPP                      | Mean phenotypic plasticity was calculated for each species averaging the values obtained from the index of phenotypic plasticity for each growth variable. This plasticity index has a range from 0 (lowest phenotypic plasticity) to 1 (highest phenotypic plasticity) was calculated as the difference between the maximum and the minimum mean values among the three nutrient treatments divided by the maximum mean value   | Valladares <i>et al.</i> (2000) |

A principal components analysis (PCA) was used to explore the interrelation and grouping among the 32 species and seed and seedling traits. For the making of the matrix, the mean value of each variable/species was employed except for the variable range of optimal temperature for germination. This trait was codified in the following categories: 1, 2, 3, and 4 for a constant temperature of 25°C and alternating temperatures of 25/30°C, 25/35°C and 25/40°C, respectively. Because of the range of several orders of magnitude, all mass variables were log transformed before analysis. PCA was performed using a correlation matrix since the variables were measured on different units, and the variable contribution in this study (i.e., the most actives) was determined by the internal correlation circle proposed by Fariñas (1996).

## RESULTS

The studied species belong to 16 families (Table 1). Fabaceae was the largest family studied, comprising eight species. The Malvaceae family was represented by four species and the Sapindaceae by three species. In 19 (59.3%) species, dispersion by animals was the most common, followed by barochory and autochory. The primary unit of dispersion in 20 (62.5%) species

was the fruit. The seeds of 20 (62.5%) species showed primary dormancy, physiological dormancy (PD) being the most common (53.1%). Physical dormancy (PY) was the main handicap for seed germination in *Albizia* and *Guazuma*, and at least a fraction of the seeds in *Lysiloma*. The seeds of *Talipariti* were the only ones in showing either PY or PD.

All variables tested played a significant role ( $P < 0.05$ ) in accordance with the internal correlation circle proposed by Fariñas (1996) in the bi-dimensional space defined by the first two principal components which explained more than 75% of the total variability of data (Fig. 1). The presence mainly of two groups of vectors located at opposite quadrants was also determined. The first group was represented by the variables PSR, GB, SMC, SDM, SRM and TSM which were positively correlated *inter se* and with the first principal component; the second was located at the quadrants III and IV, and comprised the variables VSD, SL, CGR, PSC, RGR, RLG, MPP and LRMF, which were positively correlated *inter se* and negatively with first component and variables of the first group. The second principal component was ROT, which was negatively correlated with this component and with variables PSR, GB and SMC. Also, ROT was positively correlated with variables VSD, SL, CGR, PSC and RGR.

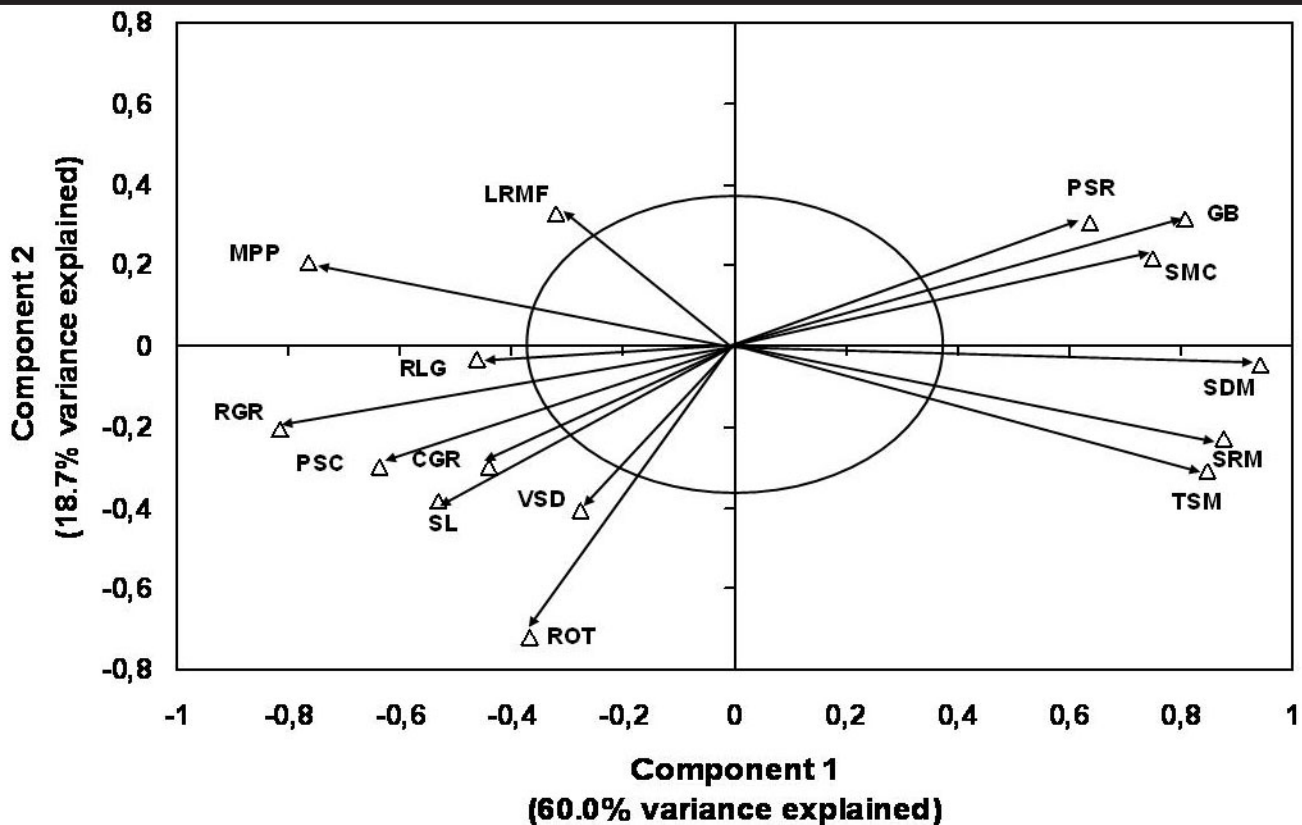


Fig. 1. Bi-dimensional principal components analysis ordination for seed and seedling variables of 32 tropical tree species. The vector corresponding to each trait indicates the directions in which variables increase and the circle of correlation establishes the value in which they started to be significant ( $P < 0.05$ ). SDM, seed dry mass; SRM, seed reserve dry mass; SMC, seed moisture content; PSC, percentage of seed dry mass in coat; PSR, percentage of seed dry mass in reserve; RLG, relative light germination index; ROT, range of optimal temperature for germination; CGR, coefficient of germination rate; GB, germination begin; VSD, variance of seed dimensions; SL, seed longevity; TSM, total seedling dry mass; RGR, relative growth rate; LRMF, lateral root mass fraction; MPP, mean phenotypic plasticity.

Likewise, the variables that contributed more (i.e., correlation) to the first component (Fig. 1) were SDM ( $r = 0.91$ ), SRM ( $r = 0.86$ ), GB ( $r = 0.84$ ), RGR ( $r = -0.81$ ) and TSM ( $r = 0.80$ ). The highest variability found in this study was exhibited by these traits (Table 3) and therefore they have contributed most to the ecological groups and inter-correlation among species. It should be pointed out that PCA also showed the establishment of correlations that were not discussed in previous paper; among the most important, the positive correlations between MPP vs. LRMF, RLG vs. CGR and VSD vs. ROT, and the negative correlations between VSD vs. PSR and VSD vs. SMC.

Geometric distance between species can be considered a measure of dissimilitude in their reproductive behavior. Three types of spatial configurations dominated the dual analysis of species and variables (Fig. 2). A first ecological group (Group I) comprises all pioneer species (*Cecropia*, *Ceiba*, *Ficus*, *Guazuma*, *Muntingia*, *Talipariti*, *Trema* and *Trichospermum*; *sensu* Herrera *et al.*, 1997) and non-pioneer species having a seed size (i.e., seed dry mass) lower than 147.0 mg (*Alchornea*, *Albizia*, *Caesalpinia*, *Colubrina*, *Cordia*, *Ehretia*, *Gliricidia*, *Lysiloma* and *Poecppigia*), this group is located where variables

SL, CGR, PSC, RGR, RLG and MPP increased (Fig. 2 and Table 3). However, according to the distribution of species, Group I can also be divided in two groups, one including the species found in the third quadrant (*Albizia*, *Caesalpinia*, *Cecropia*, *Ehretia*, *Gliricidia*, *Guazuma*, *Lysiloma*, *Poecppigia*, *Trema*, *Trichospermum* and *Talipariti*) which are characterized by the variables mentioned above and also have high values of ROT and VSD; and a second group comprising species located at the fourth quadrant (*Alchornea*, *Ceiba*, *Colubrina*, *Cordia*, *Ficus* and *Muntingia*) which had the highest values of the variable LRMF within this first great group. On the other hand, there are two groups in the quadrants I and II of the bi-dimensional space; Group III including *Andira*, *Calophyllum brasiliense*, *Calophyllum pinetorum*, *Cupania*, *Matayba*, *Ocotea*, *Prunus* and *Pseudolmedia* located towards the most opposite side from Group I and exhibiting the highest values of the variables PSR, GB, SMC, SDM, SRM and TSM. The Group II (*Allophylus*, *Bauhinia*, *Chrysophyllum*, *Psychotria*, *Samanea*, *Trichilia* and *Sideroxylon*) located near the centroid of the bi-dimensional space in an intermediate position between Groups I and III; therefore, these species had mean values in the variables used in the PCA.

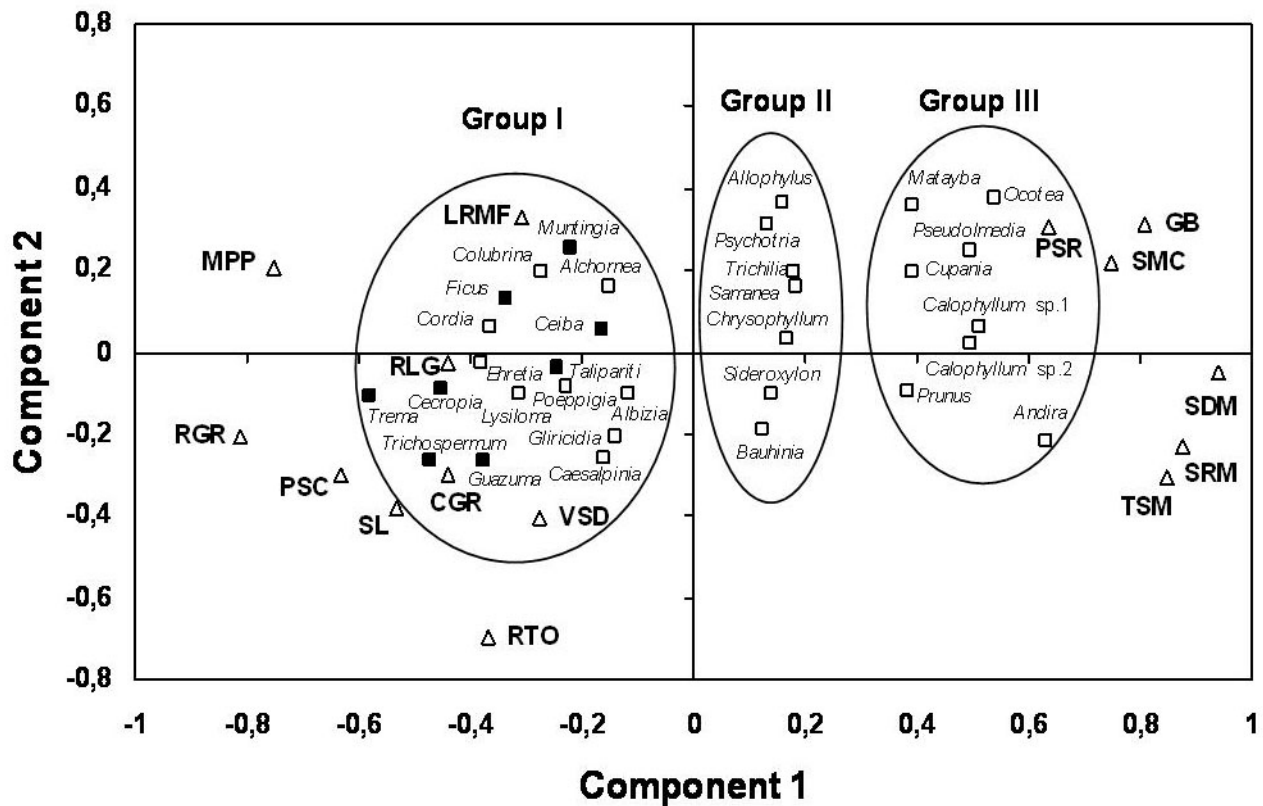


Fig. 2. Principal components analysis diagram (biplot interpretation) with 32 tropical tree species (■ and □) and variables (△). The Groups I, II, and III represent different ecological grouping. Species classified *a priori* as pioneers (*sensu* Herrera *et al.*, 1997) are shown as closes squares. Full species names as in Table 1. *Calophyllum pinetorum* and *C. brasiliense* are referred to by genus plus the codes sp.1 and sp.2, respectively. For definitions from variables see fig. 1.

Table 3. Mean of seed and seedling traits according to the different groups of ecological functioning. SDM, seed dry mass; SRM, seed reserve dry mass; SMC, seed moisture content; PSC, percentage of seed dry mass in coat; PSR, percentage of seed dry mass in reserve; RLG, relative light germination index; ROT, range of optimal temperature for germination; CGR, coefficient of germination rate; GB, germination begin; VSD, variance of seed dimensions; SL, seed longevity; TSM, total seedling dry mass; RGR, relative growth rate; LRMF, lateral root mass fraction; MPP, mean phenotypic plasticity. *n* = number of species by ecological grouping. CV = coefficient of variation in percentage.

| Variables                | Ecological functioning group |                             |                              | Total mean (CV) |
|--------------------------|------------------------------|-----------------------------|------------------------------|-----------------|
|                          | Group I<br>( <i>n</i> = 17)  | Group II<br>( <i>n</i> = 7) | Group III<br>( <i>n</i> = 8) |                 |
| SDM (mg)                 | 39.0                         | 246.7                       | 1374.2                       | 418.2 (272.3)   |
| SRM (mg)                 | 19.8                         | 127.0                       | 896.5                        | 262.5 (268.3)   |
| SMC (%)                  | 10.0                         | 12.5                        | 33.5                         | 16.9 (64.5)     |
| PSC (%)                  | 58.0                         | 39.9                        | 26.6                         | 46.2 (50.8)     |
| PSR (%)                  | 41.8                         | 60.0                        | 73.4                         | 53.6 (43.8)     |
| RLG                      | 0.64                         | 0.46                        | 0.49                         | 0.56 (31.7)     |
| ROT                      | 3.05                         | 2.57                        | 2.12                         | 2.70 (25.1)     |
| CGR (%)                  | 12.3                         | 8.75                        | 3.38                         | 9.31 (99.3)     |
| GB (day)                 | 7.20                         | 18.2                        | 35.7                         | 16.7 (119.2)    |
| VSD                      | 0.060                        | 0.048                       | 0.011                        | 0.046 (4.07)    |
| SL (month)               | 12.3                         | 6.07                        | 1.13                         | 8.17 (102.3)    |
| TSM (mg)                 | 81.2                         | 183.8                       | 511.3                        | 211.2 (170.4)   |
| RGR (day <sup>-1</sup> ) | 0.067                        | 0.022                       | 0.004                        | 0.041 (91.6)    |
| LRMF (mg/mg)             | 0.52                         | 0.46                        | 0.37                         | 0.47 (33.6)     |
| MPP                      | 0.47                         | 0.35                        | 0.31                         | 0.40 (35.4)     |

Finally, presence of seed dormancy, dispersal mode and dispersal collection were variables not dependable for the classification of species, since all succession groups showed dormancy, dispersion by animals and seed dispersion during the early rainy season. However, dormancy and seedling types are helpful for the functional classification of species. In Group I, there was a great number of species having non-dormant seeds; physical dormancy was present in this group only. Group II exhibited a similar number of physiological dormancy (PD) and non-dormant species. In Group III, all species displayed PD in at least a fraction of their seeds. In Groups I and II, seedlings with photosynthetic or nutrient-poor cotyledons predominated; whereas in Group III all species had nutrient-rich cotyledons.

## DISCUSSION

According to the results of the principal components analysis (PCA), at least three regeneration patterns or groups of ecological functioning seem to prevail among the 32 tree species tested in this study (Fig. 2). These groups were basically disposed along the first axis of the principal component which explained 60% of the total data variability. The order or grouping of species and their relations to seed and seedling traits corroborated the existence of the continuum  $r$ - $K$  in the successional strategies of tropical trees, as informed in many studies (Bazzaz, 1996; Herrera *et al.*, 1997; Muñoz, 1998; Sánchez *et al.*, 2003). In agreement with this type of classification, Odum (1969) proposed that early successional plants belong to the strategy  $r$ , and plants from more advanced stages belong to the strategy  $K$ .

In this paper, the species in Group I tend to show an “ $r$  strategy”, since all were classified *a priori* as pioneers by Herrera *et al.* (1997) and also the small-seeded non-pioneers established in open sites. Basic traits for identifying species in this group were: 1) small seeds with low moisture contents, 2) rapid germination rate, enhanced by the alternating temperatures of the substrates and/or daylight, 3) photosynthetic cotyledons (or with scarce reserves) and high rate in seedling growth, 4) high phenotypic plasticity, and 5) production of seedlings with low biomass when grown in nutrient-poor substrates. By contrast, Group III was located at the opposite extreme of the previous set, extreme where species had typical traits of the “ $K$ ” selection, such as: 1) large seeds with high moisture contents, 2) slow germination, favored basically by low temperature fluctuations, 3) cotyledons with high reserves and low growth rate of seedlings, 4) low phenotypic plasticity, and 5) seedlings with high biomass when grown in nutrient-poor substrates. The species in Group II occupy an intermediate position between Groups I and III, and showed mean values in all variables of PCA; therefore, this evidenced an intermediate position in the continuum  $r$ - $K$ . In fact, a great variety of seedling types with photosynthetic and reserve cotyledons was also observed in Group II (Table 1). The regeneration traits found in Groups I and III are characteristic for early-successional (i.e., pioneers or light demanding) or late-successional species (i.e., non-pioneers or shade-tolerant), respectively (Piña-Rodrigues *et al.*, 1990; Vázquez-Yanes and

Orozco-Segovia, 1994; Bazzaz, 1996; Cornelissen *et al.*, 1998; Herrera *et al.*, 1997; Valladares *et al.*, 2000; Kitajima, 2002; Ferraz *et al.*, 2004; Sautu *et al.*, 2006).

The existence of physical dormancy in pioneers agrees with the type of seed dormancy most frequently reported in this succession group (Vázquez-Yanes and Orozco-Segovia, 1994; Ferraz *et al.*, 2004). Likewise, Ferraz *et al.* (2004) and Sautu *et al.* (2006) informed that non-deep physiological dormancy (*sensu* Baskin and Baskin, 2004) is typical in climax or late species in forest succession. This last type of dormancy was found in climax species in this research and was also reported by Sánchez *et al.* (2007) in other tropical tree species in late stages of humid forest succession in the SRBR (e. g., *Guarea guidonia*, *Juglans insularis* and *Oxandra lanceolata*). However, results in this succession group in relation to seed dormancy contradict everything that has been published about the germination response of species in advanced stages in humid tropical forests. It has been proposed that most dominant trees in mature forests have non-dormant seeds which produce a cohort of very slow-growing seedlings (Ng, 1978; Vázquez-Yanes *et al.*, 2000), a hypothesis that has also been reported for primary tree species growing in the evergreen forests of the SRBR (Menéndez *et al.*, 1985; Herrera *et al.*, 1988b). Nevertheless, it should be pointed out that research in Cuban forests has not been based upon germination studies and therefore, it has no value for determining seed dormancy in primary species.

Several classifications have been made in order to understand the regeneration and successional strategies of tropical trees, on the base of regeneration characteristics associated to light requirements for seed germination and seedling establishment (Budowski, 1965; Denslow, 1980; Swine and Whitmore, 1988). Other classifications include seedling response to light and also the characteristics related to seed size and reserves, seed production and dispersion, seed dormancy mechanisms, fruit dimensions, formation of seed or seedling banks, growth rate of seedlings or plants, sclerophylly leaves, habitat selectivity, wood density, etc. (Herrera *et al.*, 1988b; Piña-Rodrigues *et al.*, 1990; Herrera *et al.*, 1997; Ferraz *et al.*, 2004). According to Piña-Rodrigues *et al.* (1990), the trees of Brazilian humid forests group themselves in three functional strategies or groups: Pioneers, Opportunists and Climax. However, many of these species occupy an intermediate position in the continuum of natural forest succession; therefore, they were named Opportunists-Climax (Ferraz *et al.*, 2004). In Cuba, Herrera *et al.* (1988b) also classified tropical trees from humid and dry forests of the SRBR in three groups of ecological functioning, known as Secondary, Intermediate (or Repairing) and Primary species. Taking into account their habitat preferences (e.g., humid, dry-saline or indifferent) and based upon the continuum  $r$ - $K$  of successional strategies, Herrera *et al.* (1997) grouped the successional strategies of 221 tropical trees. They remarked that there is a trend to increase selection  $K$  and decrease selection  $r$  with advancing succession and they also recognized the existence of seven main groups of strategies: Early Pioneers, Late Pioneers, Exuberants, Colonizers, Opportunists, Invaders and Austers.

In general, the groups of ecological functioning discovered in this study are in total agreement with Herrera *et al.* (1997), although different variables and exploratory methods were used for their definition. All the species in Group I occupy early-successional habitats. This group comprises pioneer species (*sensu* Herrera *et al.*, 1997) and most small-seeded non-pioneers needing light for their establishment. In this last group, there are some species considered as anthropic or invader pioneers (e.g., *Albizia*, *Caesalpinia*, and *Cordia*). Most species in Group III belong to the final successional stages (i.e., austere), which according to Herrera *et al.* (1997), grow slowly in the shade and have the greatest capacity for stability in the community. *Prunus* and *Matayba*, considered as belonging to *r-K* strategies by the above mentioned researchers, also appear in this group. These taxa were located at the order regions of the bi-dimensional space of the PCA, close to Group II. This last group included opportunists and invaders (*sensu* Herrera *et al.*, 1997), considered as *r-K*, and can occupy many microsites since they possess a highly competitive strategy.

On the other hand, the concept that species which seemingly have the same regeneration pattern also have similar physiological response lies within many schemes of classification of tropical tree strategies. However, this situation was not as evident when the order or position of many species was analyzed in each group of ecological functioning discovered in this study. In this way, the differential distribution of species along the first two axes of PCA also proved that within each group the species exhibited a species-specific response, which means that germination can take place in many microsites adequate not only for germination but also for seedling establishment. These differences in regeneration niche possibly contribute to the coexistence of these tropical tree species by reducing interspecific competition, results that have been demonstrated in many papers involving neotropical species from various environmental gradients (Denslow, 1980; Huante *et al.*, 1995; Daws, *et al.*, 2002; Pearson *et al.*, 2002; Sánchez *et al.*, 2003; Dalling *et al.*, 2004).

Finally, the results of this research corroborated the importance of seed and seedling characteristics for the definition of groups of ecological functioning of tropical species, as proposed by several workers (Martinez-Ramos *et al.*, 1989; Piña-Rodriguez *et al.*, 1990; Westoby *et al.*, 2002). Actually, there are many evidences suggesting that the patterns of distribution and abundance of tropical species are determined early in plant life-cycle (e.g., see Hubbell *et al.*, 1999).

## CONCLUSIONS AND RECOMMENDATIONS

Many of the traits in seeds and seedlings were correlated to seed size (i.e., seed dry mass or seed reserve mass), indicating that seed size could be used as a good indicator of the regeneration behavior of tropical trees under various environmental gradients (e.g., light soil and temperature, nutrient and moisture availability in the substrate). This result is normal, since seed size is an important predictor of ecological variation among species (Henery and Westoby, 2001; Westoby *et al.*, 2002; Poorter and Rose, 2005). However, the existing

correlation between seed size and seedling growth traits is not always a basic tool for the prediction of responses or adaptations of the species to the physical environment, as demonstrated by Dalling *et al.* (2004) in pioneer species responses to artificial clearings with various sizes. Also, a positive correlation between seed dry mass and germination beginning was determined in this study, which has a limited predictive value. This association indicated an increase in dormancy as seed size increases, but this does not deny the existence of small, dormant seeds (e.g., *Guazuma* and *Ehretia*). Other correlations discovered in this study, such as the relations between seed reserve mass and total dry mass reached by seedlings grown in nutrient-poor substrates, and between seed mass and the RGR under all nutrient treatments (also see Fig. 15 of Sánchez *et al.*, 2007) leave no doubt about the predictive value of seed size in the species response to nutrient variation in the substrate.

On the other hand, the results obtained from seed characterization studies, germination, dormancy and seedling establishment should contribute to the success of reforestation projects currently taking place at the SRBR, and also possibly in other Cuban regions where these native species are being used. In addition, the regeneration patterns detected or functional groups will allow the promotion of the most adequate species for forest conservation at specific sites, and management and rehabilitation of degrade areas.

Last but not least, it is important to point out that this study allowed us to discover some relations between seed size and its physical environment; however, we are far from knowing the real role of seed size in forest community in the SRBR. Laboratory and field tests related to the role of seed size in seedling establishment under several risks (i.e., defoliation, deep shade, drought, etc.), no doubt will contribute to increase our knowledge about the role of seeds in the regeneration of forest communities. Also, studies on germination, dormancy, dispersion and seed banks should be continued, all of which will support reforestation plans with native species and the conservation of tropical forests.

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