

SCIENTIFIC PAPER

Germination and dormancy of shrubs and climbing plants of the evergreen forest of Sierra del Rosario, Cuba

J. A. Sánchez¹, Laura Montejo¹, A. Gamboa¹, Delhy Albert-Puentes¹ and F. Hernández²

¹Instituto de Ecología y Sistemática-Ministerio de Ciencia, Tecnología y Medio Ambiente, Carretera de Varona 11835, Calabazar, Boyeros, La Habana 19, CP 11900, Cuba

²Reserva de la Biosfera Sierra del Rosario, Las Terrazas, Artemisa, Cuba

E-mail: jasanchez@ecologia.cu

ABSTRACT: The germination requirements and the seed dormancy classes were determined in 14 species of shrubs and climbing plants (13 vines and three lianas), of the tropical seasonal evergreen forest of the Sierra del Rosario Biosphere Reserve, Cuba. The relations between the dormancy classes and other traits of the life history of the plants were also evaluated. The germination trials were conducted under controlled laboratory conditions (light and temperature): a constant temperature of 25 °C, three conditions of alternate temperature (25/30 °C, 25/35 °C and 25/40 °C) and two light environments (light and darkness). In the shrubs, light was the main factor that regulated germination; while in the climbing plants the essayed factors did not significantly affect germination completely, although some had a species-specific response. Only two species were totally positive photoblastic, and the germination under light decreased with the fresh seed mass. Dormancy occurred in 23 species (76,6 %), from them 10 were shrubs and 13, climbing plants. In the shrubs the physiological dormancy was the most abundant, and in the climbing plants, the physiological and physical dormancy prevailed. Among the climbing plants the only species with morphological and/or morphophysiological dormancy were found. The highest number of dormant seeds was observed in the dry season (87 %). The study confirmed the diversity of dormancy mechanisms and germination requirements already reported in these life forms for the tropics.

Key words: vines, lianas, seed, viability

INTRODUCTION

The natural regeneration cycle of the plant populations is a concatenated series of demographic processes (seed production, dispersal, germination, emergence and establishment of the new seedling), which responds to the current environmental variability (abiotic and biotic factors) and to the historical climate changes (Marañón *et al.*, 2008). These biological processes, dependent on the microhabitat and the evolutionary mechanisms that minimize the risk of transition from seeds to seedlings, are under the influence of the selection pressure (Kos, Baskin and Baskin, 2012). According to Baskin and Baskin (2004), the natural selection pressure should favor germination, dormancy and longevity patterns that increase the success of the establishment of the new seedling in a certain environment. However, there is a high mortality rate of seedlings under natural conditions and in nursery (Norden *et al.*, 2009); hence the knowledge of the dormancy classes and the germination requirements would allow to increase the success of the tropical restoration plans (Baskin and Baskin, 2005). Nevertheless, this knowledge is very scarce for the native species of

Neotropic forests, and a large part of the existing information is related to plants of forestry interest (Sánchez *et al.*, 2011). In this sense, the first report about the seed dormancy classes in communities of tropical trees of semideciduous forests in Panama was made by Sautu *et al.* (2007).

In Cuba, these studies are also very restricted; there is only one contribution by Sánchez *et al.* (2012) about 60 tree species from the seasonal evergreen forest of the Sierra del Rosario Biosphere Reserve (SRBR), while the regeneration mechanisms of other life forms such as shrubs, lianas and vines have not been studied. Thus, it would be relevant to study their germination requirements, the dormancy classes and other life traits at community level. This knowledge would help in the conservation of Cuban native plants –especially the ones in danger of extinction–, because, according to Baskin and Baskin (1998), it would allow to predict the most favorable periods for the establishment of seedlings in nature, to know the trend of the species to form transitory or persistent seed banks, depending on the existence or absence of dormancy/latency and the attainment of seedlings under nursery condi-

tions; as well as to conduct facultative germination essays before the conservation of seeds in germplasm banks.

According to these premises, the objectives of the work were: 1) to determine the way in which the substratum temperature and light affect the germination of shrubs and climbing plants of a tropical evergreen forest of the SRBR, 2) to identify the seed dormancy classes, and 3) to determine the relations that are established between the dormancy classes and other life history traits.

MATERIALS AND METHODS

Site description. The SRBR is located in the easternmost part of Sierra del Rosario, Artemisa, Cuba (22° 45' N, 82° 50' W) and has an extension of 25 000 ha. In the region, the mean annual temperature of the air is 24,4 °C. The minimum and maximum temperature values for the soil of the understory at 2 cm of depth during the summer (May-October) are 22,3 and 24,5 °C; while for a large clearing in the canopy they are 22,5 and 34,5 °C, respectively (Herrera *et al.*, 1988). The average annual rainfall is 2 300 mm, and, according to the rainfall distribution and the proposal made by Sánchez *et al.* (2009), three dispersal/collection seasons were acknowledged: dry season (DS, December-March), early rainy season (ERS, April-July) and late rainy season (LRS, August-November).

Selected species and seed collection. The plants were selected based on their frequency in the studied site and the seed availability. According to Herrera *et al.* (1988), the species belong to the primary flora of the SRBR forests (table 1), except *Indigofera suffruticosa*, which is a naturalized species for this site. The species were arranged from the average value of the seed fresh mass within each life form (Montejo *et al.*, 2014a), which showed a wide range of values (0,042-5 526,0 mg). The names of the plants were established according to the report by Acevedo-Rodríguez and Strong (2012) and in the case of the botanical families the The Angiosperm Phylogeny Group (2003) was followed. The taxa belonged to 18 botanical families, the most represented ones were: *Fabaceae* (6) and *Solanaceae* (3). Fresh seeds of 14 shrub and 16 climbing species (13 vines and three lianas) were collected.

The type of diaspore (dispersal unit) of 21 species was the fruit. In this study, a true seed was considered as seed and a true seed plus the endocarp was considered as diaspore. The species whose diaspore included the endocarp of the drupes were:

Gonzalagunia sagreana, *Bourreria cassinifolia*, *Clerodendrum grandiflorum*, *Malpighia glabra* and the endocarp of the chamber was found in *Turbina corymbosa*.

The seeds were collected at the Ecological Station El Salón (central section of the SRBR), surrounded by a submontane seasonal evergreen forest, with a closed canopy of 30-m of height and 13 % of trees that lose their leaves during the months of lower rainfall. All the fruits of five or more healthy individuals were directly taken from the mother plant, with a telescopic rod, and were immediately cleaned. The seeds were dried during 72 h, in the air and under shade.

Germination requirements. The seeds of each species were mixed and sown during the first three days, after they were cleaned. The germination studies were conducted in incubators, with controlled light and temperature. A completely randomized design was used, with factorial arrangement of the treatments, which simulated the variations of light and temperature undergone by the forest from a clearing to its deep areas. Four temperature and two light conditions were tested, for a total of eight treatments per species. The germination responses were obtained at constant temperature of 25 °C and in a regime of alternate temperature of 25/30 °C, 25/35 °C and 25/40 °C (8 h for the highest temperature of the thermoperiod and 12 h at 25 °C, with a transition of 4 h between them). The light treatments were: exposure to light (8 hours of approximately 40 $\mu\text{mol m}^{-2} \text{s}^{-1}$, length of 400-700 nm), coinciding with the period of highest temperature within each thermoperiod; and constant darkness. This last condition was achieved wrapping the plates in two layers of aluminum foil. The location of the plates in the incubator was regularly changed.

Before sowing, the seeds were sterilized with mercuric chloride (1 g L⁻¹), to prevent fungal contamination. Five replications of 25 seeds each were used per treatment. The sowing was made on 1 % hydrostatic agar, on Petri dishes of 9 or 15 cm diameter, depending on the seed size. In the case of the seeds that were illuminated, the germination count was made every day during 30 to 90 days, depending on the species. In the seeds exposed to continuous conditions of total darkness, the count was made three days after concluding germination under light. The criterion for considering the seeds germinated was the protrusion of the radicle. In the treatments under light, the agar was maintained moist during the trial.

Table 1. Life history traits of 30 shrub and climbing species of the SRBR.

Species/life form	Botanical family	Seed mass (mg)	Fruit type	Diaspore type
Shrubs				
<i>Gonzalagunia sagreana</i> Urb. [▲]	<i>Rubiaceae</i>	0,042	Drupe	Fruit
<i>Conostegia xalapensis</i> (Bonpl.) D. Don	<i>Melastomataceae</i>	0,08	Berry	Fruit
<i>Pluchea carolinensis</i> (Jacq.) G. Don	<i>Asteraceae</i>	0,32	Cypsela	Seed
<i>Chromolaena odorata</i> (L.) R.M. King & H. Rob	<i>Asteraceae</i>	0,34	Cypsela	Seed
<i>Hyptis verticillata</i> Jacq.	<i>Lamiaceae</i>	0,52	Capsule	Fruit
<i>Solanum jamaicense</i> Mill.	<i>Solanaceae</i>	0,82	Berry	Fruit
<i>Solanum torvum</i> Dund	<i>Solanaceae</i>	1,25	Berry	Fruit
<i>Indigofera suffruticosa</i> Mill.	<i>Fabaceae</i>	3,68	Pod	Seed
<i>Cestrum laurifolium</i> L'Hér	<i>Solanaceae</i>	8,75	Berry	Fruit
<i>Psychotria domingensis</i> Jacq.	<i>Rubiaceae</i>	16,3	Berry	Fruit
<i>Bourreria cassinifolia</i> (Wild) Miers	<i>Boraginaceae</i>	22,6	Drupe	Fruit
<i>Clerodendrum grandiflorum</i> (Hook.) Schauer*	<i>Verbenaceae</i>	39,9	Drupe	Fruit
<i>Ardisia dentata</i> (A.DC.) Mez.*	<i>Myrsinaceae</i>	46,6	Berry	Fruit
<i>Malpighia glabra</i> L.	<i>Malpighiaceae</i>	62,1	Drupe	Fruit
Climbing species				
<i>Jacquemontia verticillata</i> (L.) Urb.	<i>Convolvulaceae</i>	2,05	Capsule	Fruit
<i>Passiflora sexflora</i> Juss	<i>Passifloraceae</i>	2,27	Berry	Fruit
<i>Passiflora suberosa</i> L.	<i>Passifloraceae</i>	3,25	Berry	Fruit
<i>Gouania lupuloides</i> (L.) Urb.	<i>Rhamnaceae</i>	3,33	Samara	Fruit
<i>Dioscorea tamoidea</i> Griseb	<i>Discoriaceae</i>	7,13	Capsule	Fruit
<i>Lasiacis divaricata</i> (L.) Hitch.	<i>Poaceae</i>	7,46	Caryopsis	Fruit
<i>Davila rugosa</i> Poir.	<i>Dilleniaceae</i>	9,82	Capsule	Seed
<i>Rhynchosia reticulata</i> (Sw.) DC.	<i>Fabaceae</i>	22,8	Pod	Seed
<i>Turbina corymbosa</i> (L.) Raf.	<i>Convolvulaceae</i>	34,4	Chamber	Fruit
<i>Clitoria ternatea</i> L.	<i>Fabaceae</i>	49,7	Pod	Seed
<i>Smilax mollis</i> Humb. & Bonpl. Ex Willd.	<i>Smilacaceae</i>	53,7	Berry	Fruit
<i>Cayaponia racemosa</i> (Mill.) Cong.	<i>Cucurbitaceae</i>	57,4	Berry	Fruit
<i>Smilax laurifolia</i> L.	<i>Smilacaceae</i>	79,1	Berry	Fruit
<i>Abrus precatorius</i> L.	<i>Fabaceae</i>	90,5	Pod	Seed
<i>Bauhinia glabra</i> Jacq.	<i>Fabaceae</i>	145,4	Pod	Seed
<i>Mucuna pruriens</i> (L.) DC.	<i>Fabaceae</i>	5 526,0	Pod	Seed

▲Cuban endemisms.

The final germination percentage in light and in darkness was determined. In the seeds germinated in the light the day of starting germination (SDG) and the germination rate coefficient (GRC) were also established. The GRC was calculated for each replica, dividing the final number of germinated seeds (N) between the summation of the

number of germinated seeds in a particular day (n_i), multiplied by the corresponding number of days (d_i) since the beginning of the experiment (Alm *et al.*, 1993): $GRC = N / \sum n_i d_i$. The GRC values were found between 0 (no germination) and 1 (fast germination rate), and were multiplied by 100 to facilitate the interpretation.

The final germination percentage in the light and the darkness was used to calculate the index of germination relative to light (GRL), which expressed the light requirements for germination (Milberg, Andersson and Thompson, 2000). This index was calculated according to the formula: $GRL = GL / (GD + GL)$, where GL: germination percentage in the light, and GD: germination percentage in the darkness. To obtain the GRL index of each species the optimum temperature range (i.e., that in which the species showed the highest germination percentage in the light or in the darkness) was used. The GRL values varied between 0 (seeds that germinate only in the darkness) and 1 (seeds that germinate only in the light).

In the case of the seeds that did not germinate, the viability was determined through the TZ test (ISTA, 1999); or pressing the seeds with a needle to determine whether they contained a white and firm embryo (living seeds) or a gray and soft one (absence of seed viability).

Assignment of the dormancy classes. It was considered that one species had dormant seeds if: a) their germination started after 28 days under optimum conditions (Baskin and Baskin, 1998), b) the seeds had underdeveloped and differentiated embryos (i.e., the embryo should grow inside the seed), independently from the time to start germination; c) at least 20 % of the seeds remained alive and non-germinated. The seeds were considered non-dormant if the embryo was completely developed and they required less than 28 days to germinate (Baskin and Baskin, 1998).

The species with dormant seeds were classified according to the system of seed dormancy classes proposed by Baskin and Baskin (2004), which acknowledges five classes: 1) physiological dormancy (PD), 2) morphological dormancy (MD), 3) morpho-physiological dormancy (MPD), 4) physical dormancy (PY), and 5) combined dormancy (PY + PD). The seeds which have combined dormancy need more than 28 days to germinate, after PY is eliminated.

The water absorption capacity (imbibition) of the fresh seeds was determined in those species whose germination percentages were low, or rather in those in which PY is reported in the family. For such purpose, five replicas of 25 seeds per species were used, which were placed on two layers of filter paper moist with distilled water on Petri dishes. The tests were conducted under white light and at the optimum germination temperature of each spe-

cies (as it was previously described). At 24, 48 and 72 hours of imbibition, the seeds were superficially dried and weighed. The water absorption percentage was determined with relation to the fresh weight of the seeds.

In the cases in which the germination percentages were low and the number of collected seeds was sufficient, pre-germination treatments were also applied, in order to break the seed dormancy. These treatments were: total mechanical scarification (TMS) in *Ardisia dentata*, *B. cassinifolia*, *Clerodendrum grandiflorum* and *Cestrum laurifolium*, and testa rupture in *Mucuna pruriens*. The essays were performed under the optimum germination conditions of each species, which were established in the germination tests without treatments. The final germination percentage and the starting day of germination were determined.

Finally, to assign the dormancy classes not only the above-referred methodologies were used, but also the information about the type of embryo reported for the species/family and the morphological characteristics of the seeds, because the seed dormancy is a highly preserved phylogenetic trait (Baskin and Baskin, 2005; Kos *et al.*; 2012).

Life history traits per dormancy class. The seed variables compared were: seed fresh mass (mg), initial moisture content (%), seed dry mass percentage destined to seed coats, GRL index, SDG and final germination percentage (FG). The seed traits were taken from the report by Montejo *et al.* (2014a), and the germination traits, from this study. The dormancy classes were also determined according to the time and form of seed dispersal. To assign the dispersal syndromes the species were grouped in two categories: the ones that were dispersed by the animals (including the internal or external dispersal) and those which were not dispersed by these animals.

Statistical analysis. The germination traits that were established at community level and per life form did not fulfill the premises of the parametric assumptions; thus, to detect possible interactions between the factors (temperature by light), a multivariate variance analysis based on permutations –PERMANOVA– (Anderson, 2001) was applied. The PERMANOVA were made with the mean value of each species and by a matrix of Euclidian distance, after 9 999 interactions. To study the relation between the seed mass (seed size) and the GRL index, a simple linear regression analysis was used. The differences between the imbibition

times and the pre-germination treatments were detected through a simple classification ANOVA, because the data fulfilled the premises of this analysis. In addition, a one-way similarity analysis (ANOSIM) was used, to evaluate the H_0 hypothesis of no statistically significant differences among life history traits per dormancy classes. Each ANOSIM was performed with a matrix of Euclidian distance and using 9 999 permutations.

RESULTS

Germination requirements. The germination of the 30 species was significantly affected by temperature ($F_{(3, 232)} = 2,82$; $p < 0,05$) and the light of

the substratum ($F_{(1, 232)} = 11,07$; $p < 0,001$), although no interaction was observed between these factors ($p = 0,83$). Light was the most important factor, for which the darkness conditions considerably affected germination (fig. 1A). When considering the total of species, the FG percentage at 25/30 °C and 25/35 °C was higher than at constant temperature (25 °C), in the light as well as in the permanent darkness; but did not differ from that obtained at 25/40 °C. In the shrubs, this general pattern was repeated (fig. 1B), that is, germination depended significantly on temperature ($F_{(3, 104)} = 4,05$; $p < 0,01$) and on the substratum light ($F_{(1, 104)} = 21,90$; $p < 0,001$), but not

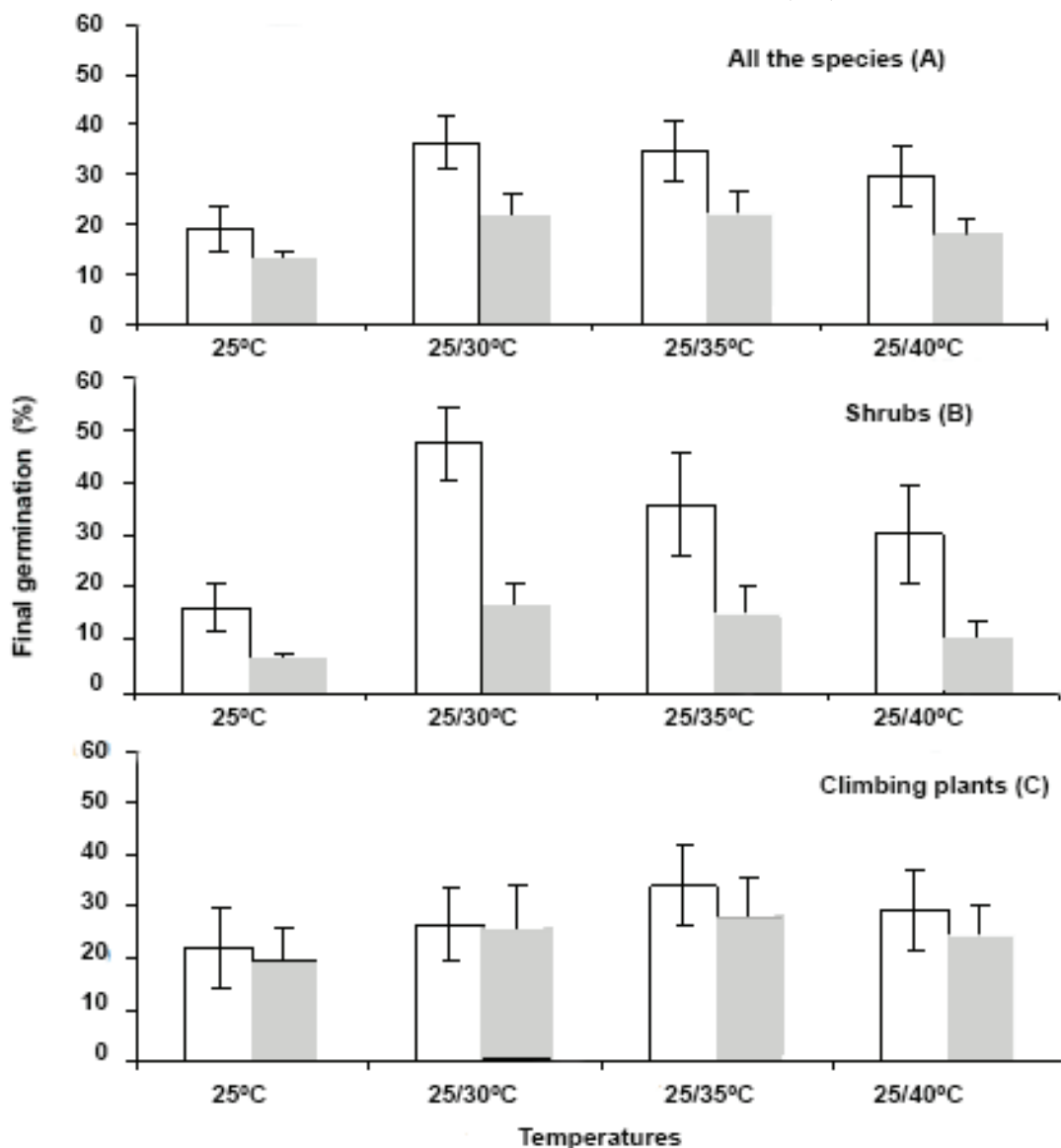


Figure 1. FG percentage (mean + SE), according to temperature, in the light (white bars) and in the permanent darkness (black bars).

on the interaction of these factors ($p = 0,91$). The increase of germination in the shrubs because of light was more evident in the range of 25/30 °C, although it did not differ from the results obtained at 25/35 °C and 25/40 °C, but it did at 25 °C. In the climbing plants, the ANOVA did not show differences in the final germination (data not shown), although the maximum average value was found at 25/35 °C under white light (fig. 1C).

The pattern for all the taxa was also individually repeated in many shrub as well as climbing species (table 2). However, in seven shrub species (*G. sagreana*, *Conostegia xalapensis*, *Pluchea carolinensis*, *Chromolaena odorata*, *Hyptis verticillata*, *Solanum jamaicense* and *Solanum torvum*) which grew from small seeds (less than 1,3 mg, table 1) germination was null, when sowing was performed

Table 2. Final germination percentage (mean $\pm$ SE) under different sowing conditions.

Species	Light				Darkness			
	25 °C	25/30 °C	25/35 °C	25/40 °C	25 °C	25/30 °C	25/35 °C	25/40 °C
Shrubs								
<i>G. sagreana</i>	0	48,3 $\pm$ 6,0	42,2 $\pm$ 5,8	6,0 $\pm$ 0,5	0	0	0	0
<i>C. xalapensis</i>	9,2 $\pm$ 1,4	21,2 $\pm$ 1,9	26,4 $\pm$ 1,4	12,9 $\pm$ 3,6	0	0	14,2 $\pm$ 0,8	5,6 $\pm$ 1,5
<i>P. carolinensis</i>	13,3 $\pm$ 3,8	53,0 $\pm$ 0,0	93,1 $\pm$ 4,0	77,7 $\pm$ 5,8	0	0	46,6 $\pm$ 3,1	22,0 $\pm$ 2,0
<i>C. odorata</i>	50,0 $\pm$ 8,8	82,5 $\pm$ 1,4	53,7 $\pm$ 7,7	52,5 $\pm$ 9,2	0	5,0 $\pm$ 1,0	0	0
<i>H. verticillata</i>	54,6 $\pm$ 1,7	66,6 $\pm$ 1,2	70,6 $\pm$ 2,6	69,3 $\pm$ 2,6	0	24,3 $\pm$ 3,2	35,8 $\pm$ 1,3	33,3 $\pm$ 2,4
<i>S. jamaicense</i>	0	68,6 $\pm$ 11,5	75,3 $\pm$ 13,6	75,3 $\pm$ 2,3	0	5,6 $\pm$ 1,2	17,7 $\pm$ 4,4	26,6 $\pm$ 3,8
<i>S. torvum</i>	0	98,3 $\pm$ 1,6	96,6 $\pm$ 3,3	88,6 $\pm$ 6,6	0	0	61,6 $\pm$ 10,1	33,3 $\pm$ 7,2
<i>I. suffruticosa</i>	10,0 $\pm$ 2,8	6,6 $\pm$ 1,6	18,3 $\pm$ 2,3	35,0 $\pm$ 5,7	7,3 $\pm$ 1,8	11,6 $\pm$ 4,4	18,3 $\pm$ 3,3	21,6 $\pm$ 1,6
<i>C. laurifolium</i>	6,6 $\pm$ 1,6	56,6 $\pm$ 5,6	13,3 $\pm$ 3,3	3,3 $\pm$ 0,3	7,8 $\pm$ 3,2	50,3 $\pm$ 2,3	8,3 $\pm$ 1,4	0
<i>P. domingensis</i>	14,6 $\pm$ 1,3	38,3 $\pm$ 3,1	10,3 $\pm$ 0,3	0	9,8 $\pm$ 1,3	26,7 $\pm$ 2,1	3,0 $\pm$ 1,2	0
<i>B. cassinifolia</i>	11,0 $\pm$ 5,5	27,7 $\pm$ 3,5	0	0	8,3 $\pm$ 1,3	29,3 $\pm$ 3,1	0	0
<i>C. grandiflorum</i>	20,0 $\pm$ 1,9	33,3 $\pm$ 6,2	0	0	15,1 $\pm$ 2,3	24,3 $\pm$ 1,3	0	0
<i>A. dentata</i>	13,3 $\pm$ 3,3	26,6 $\pm$ 3,1	0	0	12,8 $\pm$ 1,3	20,3 $\pm$ 3,1	0	0
<i>M. glabra</i>	23,4 $\pm$ 1,3	35,8 $\pm$ 1,3	0	0	19,3 $\pm$ 2,0	33,3 $\pm$ 4,1	0	0
Climbing plants								
<i>J. verticillata</i>	21,6 $\pm$ 7,2	40,0 $\pm$ 2,	53,3 $\pm$ 4,4	60,0 $\pm$ 2,8	20,1 $\pm$ 2,1	15,8 $\pm$ 4,2	33,1 $\pm$ 3,1	48,3 $\pm$ 4,4
<i>P. sexflora</i>	0	4,4 $\pm$ 2,2	73,0 $\pm$ 7,5	68,8 $\pm$ 8,0	0	0	84,4 $\pm$ 2,2	46,6 $\pm$ 5,8
<i>P. suberosa</i>	0	10,0 $\pm$ 0,0	35,0 $\pm$ 4,0	0	0	0	23,1 $\pm$ 1,0	0
<i>G. lupuloides</i>	77,7 $\pm$ 11,1	33,3 $\pm$ 0,0	0	0	68,3 $\pm$ 3,0	30,3 $\pm$ 2,3	0	0
<i>D. tamoidea</i>	53,3 $\pm$ 3,3	67,8 $\pm$ 1,3	36,6 $\pm$ 3,3	10,0 $\pm$ 5,3	42,8 $\pm$ 1,2	63,4 $\pm$ 3,3	26,3 $\pm$ 1,3	12,3 $\pm$ 2,1
<i>L. divaricata</i>	0	16,6 $\pm$ 0,	27,7 $\pm$ 5,5	5,5 $\pm$ 1,6	0	0	0	0
<i>D. rugosa</i>	0	0	35,5 $\pm$ 9,9	16,6 $\pm$ 0,8	0	0	32,3 $\pm$ 1,3	10,7 $\pm$ 3,2
<i>R. reticulata</i>	0	21,3 $\pm$ 2,6	38,3 $\pm$ 0,3	43,6 $\pm$ 1,3	0	19,4 $\pm$ 3,4	38,3 $\pm$ 1,4	40,3 $\pm$ 3,4
<i>T. corymbosa</i>	0	6,5 $\pm$ 2,6	11,9 $\pm$ 4,7	48,2 $\pm$ 10,9	0	3,4 $\pm$ 0,3	12,3 $\pm$ 2,8	39,3 $\pm$ 1,8
<i>C. ternatea</i>	66,6 $\pm$ 12,9	81,6 $\pm$ 6,5	63,1 $\pm$ 6,4	36,7 $\pm$ 8,0	59,9 $\pm$ 8,6	80,3 $\pm$ 2,3	50,3 $\pm$ 3,8	35,3 $\pm$ 4,1
<i>S. mollis</i>	23,3 $\pm$ 4,3	16,6 $\pm$ 6,6	0	0	26,4 $\pm$ 1,6	8,7 $\pm$ 3,1	0	0
<i>C. racemosa</i>	0	33,3 $\pm$ 6,6	0	0	0	100 $\pm$ 0	0	0
<i>S. laurifolia</i>	16,6 $\pm$ 3,3	6,6 $\pm$ 1,5	0	0	20,0 $\pm$ 2,5	10,3 $\pm$ 1,8	0	0
<i>A. precatarius</i>	5,0 $\pm$ 0,5	1,6 $\pm$ 1,3	71,8 $\pm$ 8,6	90,0 $\pm$ 0,4	0	0	53,8 $\pm$ 2,1	73,3 $\pm$ 3,3
<i>B. glabra</i>	85,0 $\pm$ 2,3	85,0 $\pm$ 3,4	95,0 $\pm$ 1,3	75,0 $\pm$ 3,2	70,3 $\pm$ 1,8	76,3 $\pm$ 2,4	90,5 $\pm$ 0,4	60,3 $\pm$ 1,4
<i>M. pruriens</i>	0	0	0	13,0 $\pm$ 6,6	0	0	0	10,6 $\pm$ 2,3

under conditions of total darkness and at 25 °C. Likewise, it was proven, independently from the condition of substratum light, that the best germination response in 11 species (36,6 %) occurred at 25/30 °C; while in 9 species (30,0 %) it was shown at 25/35 °C. At 25 °C, the best germination (10,0 %) was reached in only 3 climbing species (*Gouania lupuloides*, *Smilax mollis* and *Smilax laurifolia*) and at 25/40 °C, in 7 species (23,3 %), from them two shrubs (*S. jamaicense* and *I. suffruticosa*) and 5 climbing plants (*Jacquemontia verticillata*, *Rhynchosia reticulata*, *T. corymbosa*, *Abrus precatorius* and *M. pruriens*).

There was not a clear pattern between the fresh mass of the seed (size) and the FG percentage, although this last variable tended to be minimal when the alternance of the substratum temperature and the seed size were increased. This effect was higher in the shrubs under light as well as under darkness conditions (table 2).

The GRC and SDG did not show significant differences ($p = 0,45$ and $p = 0,79$, respectively) in the different temperatures, according to the results of the ANOVA, but they did not show the true differences caused by the substratum temperatures in the germination process rate (table 3). The GRC and SDG were only recorded for 11 species from the 30 studied ones. The highest GRC values (fast germination rate) and the lowest SDG values (lowest time to start germination) were obtained at the optimum germination temperature of each species.

Under the optimum sowing conditions, the FG percentage among the species varied from 13,0 % in *M. pruriens* to 96,6 % in *S. torvum*; 13 species (which represented 43,3 %) reached more than 50 % germination and only 4 (13,3 %) achieved less than 30 % in this variable. The GRC (%) oscillated from 0,7 in *M. pruriens* to 26,9 in *C. odorata*, and the SDG comprised from 2,2 days in *C. odorata* to 97,3 days in *Davila rugosa* (table 3). In the shrubs, the GRC and SDG showed moderate values of $7,2 \pm 1,8$ % and $23,3 \pm 6,5$ days, respectively; while in the climbing plants these variables were $3,5 \pm 0,7$ % and $34,8 \pm 2,8$ days, respectively.

The percentage of non germinated living (or dormant) seeds, in all the species, was only significantly affected by the substratum temperature ($F_{(3, 231)} = 2,93, p < 0,05$); and when the analysis per life form was performed none of the tested factors or their interaction significantly affected such variable (data not shown).

The percentage of dormant seed, in the optimum temperature range for the germination of each

species, also varied considerably, from 0 % in diverse species to 83 % in *S. laurifolia* (table 4). Nevertheless, the null values in some species (e.g., *G. sagreana*, *Psychotria domingensis*, *B. cassinifolia*, *C. grandiflorum*, *A. dentata*, *M. glabra*, *Passiflora suberosa* and *Lasiacis divaricata*) and very low in others did not really represent the dormancy degree; in these species the sowing conditions affected the viability of the seeds that could not germinate.

The GRL, which represented the relation between the germination percentage in the light and in the darkness, varied from 0, 24 to 1. This last value was reached by only two species (*G. sagreana* and *L. divaricata*), which could be considered light-dependent to germinate or positive photoblastic; and the seeds from *C. odorata* and *S. jamaicense* can be also included in this group due to their high GRL values (0,94 and 0,73, respectively). In general, these species showed small seeds (with a weight lower than 2,5 mg). Likewise, 9 species appeared (*C. xalapensis*, *P. carolinensis*, *H. verticillata*, *S. torvum*, *I. suffruticosa*, *P. domingensis*, *C. grandiflorum*, *A. dentata* and *P. suberosa*) which germinated better in the light than in the darkness, but the GRL values were not so high (0,56-0,67). On the other hand, the only species that showed a GRL value lower than or equal to 0,40 was *Cayaponia racemosa* (0,24), taxon which prefers the darkness to germinate; although curiously the other two studied lianas (*S. mollis* and *S. laurifolia*: 0,46 and 0,45, respectively) and the vine *Passiflora sexflora* (0,46) also showed low values of the GRL index, which were located within the range of species indifferent to light, but tended to germinate better in the darkness (table 2).

The other species (13-43 % of the total) germinated similarly under light or darkness conditions (indifferent to light); the GRL values varied from 0,48 to 0,55, and the seed mass, from 2,0 to 5 226,0 mg; although, as average, the ones that integrated this group showed a fresh seed mass of 382,5 mg. In all the species, the GRL index was negatively related to the fresh seed mass (fig. 2; $R^2 = 0,339, p < 0,001$), that is, the germination response to light decreased with the increase of the seed mass.

Assignment of the dormancy classes. From the 30 studied species, 23 (76,6 %) had dormant seeds. From them, 10 were shrubs (43,47 %) and 13, climbing plants (56,53 %). The taxa with non-dormant seeds (*P. carolinensis*, *C. odorata*, *S. jamaicense*, *S. torvum*, *G. lupuloides*, *Clitoria ternatea* and *Bauhinia glabra*) showed as average $85,9 \pm 8,7$ % of FG

Table 3. Mean values of the germination rate coefficient and of the starting day of germination.

Species	GRC (%)				SDG (days)			
	25 °C	25/30 °C	25/35 °C	25/40 °C	25 °C	25/30 °C	25/35 °C	25/40 °C
Shrubs								
<i>G. sagreana</i>	–	1,7 ± 0,1	1,5 ± 0,0	1,2 ± 0,1	–	36,0 ± 3,0	53,3 ± 2,3	80,0 ± 1,0
<i>C. xalapensis</i>	4,6 ± 0,8	13,3 ± 0,4	13,2 ± 0,5	9,1 ± 2,3	25,0 ± 1,9	6,0 ± 0,3	7,0 ± 0,4	24,2 ± 4,0
<i>P. carolinensis</i>	5,2 ± 0,4	11,7 ± 1,3	10,6 ± 1,8	3,2 ± 0,0	16,3 ± 4,6	7,0 ± 0,0	7,0 ± 0,0	7,0 ± 0,5
<i>C. odorata</i>	21,7 ± 2,2	26,9 ± 3,0	23,6 ± 2,4	13,5 ± 2,	4,0 ± 0,0	2,2 ± 0,2	2,2 ± 0,2	6,0 ± 1,0
<i>H. verticillata</i>	2,9 ± 0,1	4,6 ± 0,3	5,3 ± 0,7	5,0 ± 0,2	13,3 ± 1,7	9,3 ± 1,3	8,6 ± 1,6	12,0 ± 0,0
<i>S. jamaicense</i>	–	5,6 ± 0,1	6,3 ± 0,1	7,3 ± 1,3	–	13,0 ± 1,0	16,0 ± 0,6	9,6 ± 1,3
<i>S. torvum</i>	–	11,6 ± 0,3	13,0 ± 0,6	12,4 ± 0,8	–	7,0 ± 0,5	6,0 ± 0,4	7,0 ± 0,8
<i>I. suffruticosa</i>	2,7 ± 0,9	9,1 ± 4,5	5,3 ± 1,3	2,5 ± 0,8	46,3 ± 31,3	32,3 ± 24,3	24,8 ± 12,1	6,6 ± 0,8
<i>C. laurifolium</i>	2,3 ± 1,2	5,0 ± 0,2	3,3 ± 0,7	0,5 ± 0,2	21,0 ± 5,0	13,0 ± 1,5	43,3 ± 3,6	57,0 ± 3,5
<i>P.domingensis</i>	2,0 ± 1,1	3,8 ± 1,4	0,9 ± 0,5	–	64,3 ± 1,3	41,8 ± 2,7	67,8 ± 1,1	–
<i>B. cassinifolia</i>	1,1 ± 1,3	2,3 ± 0,6	–	–	77,3 ± 8,6	70,0 ± 7,5	–	–
<i>C.grandiflorum</i>	1,6 ± 0,2	2,7 ± 0,8	–	–	61,6 ± 8,3	45,0 ± 0,5	–	–
<i>A. dentata</i>	2,9 ± 0,6	2,2 ± 0,1	–	–	41,3 ± 9,2	35,3 ± 2,3	–	–
<i>M. glabra</i>	1,0 ± 3,2	3,6 ± 0,8	–	–	54,3 ± 1,8	39,3 ± 2,3	–	–
Climbing plants								
<i>J. verticillata</i>	2,0 ± 0,1	1,6 ± 0,4	1,8 ± 0,1	2,4 ± 0,6	17,6 ± 3,3	25,3 ± 1,3	22,0 ± 4,1	12,0 ± 1,0
<i>P. sexflora</i>	–	1,9 ± 0,6	1,5 ± 0,0	1,5 ± 0,0	–	65,0 ± 14,0	46,0 ± 6,0	53,0 ± 2,5
<i>P. suberosa</i>	–	2,3 ± 0,9	1,4 ± 0,1	–	–	47,5 ± 11,3	42,0 ± 0,5	–
<i>G. lupuloides</i>	2,2 ± 1,1	4,5 ± 0,8	–	–	21,0 ± 2,8	23,6 ± 3,9	–	–
<i>D. tamoides</i>	2,3 ± 0,6	2,8 ± 1,3	1,7 ± 0,5	1,3 ± 0,3	40,6 ± 3,6	35,7 ± 3,1	79,0 ± 15,0	121,0 ± 0,2
<i>L. divaricata</i>	–	3,5 ± 0,2	2,8 ± 0,9	1,9 ± 0,9	–	28,3 ± 2,3	23,0 ± 3,0	34,3 ± 4,1
<i>D. rugosa</i>	–	–	1,3 ± 0,2	1,0 ± 0,0	–	–	97,3 ± 10,6	90,6 ± 17,3
<i>R. reticulata</i>	–	3,6 ± 1,2	4,6 ± 2,3	5,6 ± 3,1	–	28,3 ± 1,3	23,5 ± 2,1	17,8 ± 3,4
<i>T. corymbosa</i>	–	4,6 ± 1,8	5,2 ± 2,7	2,3 ± 0,4	–	16,5 ± 3,7	26,5 ± 7,7	12,5 ± 1,4
<i>C. ternatea</i>	7,0 ± 0,4	10,4 ± 1,2	5,3 ± 0,3	6,2 ± 0,0	6,0 ± 0,0	3,7 ± 0,3	4,0 ± 0,7	11,5 ± 2,5
<i>S. mollis</i>	3,0 ± 0,8	3,2 ± 1,2	–	–	43,3 ± 1,3	50,3 ± 1,6	–	–
<i>C. racemosa</i>	–	5,8 ± 1,3	–	–	–	29,0 ± 1,0	–	–
<i>S. laurifolia</i>	1,7 ± 0,3	0,9 ± 0,4	–	–	73,6 ± 7,2	93,3 ± 3,3	–	–
<i>A. precatorius</i>	8,0 ± 1,0	7,6 ± 3,1	2,1 ± 0,2	2,1 ± 0,0	12,6 ± 1,4	13,0 ± 0,0	23,6 ± 7,0	28,0 ± 9,0
<i>B. glabra</i>	10,1 ± 3,1	5,6 ± 1,3	9,1 ± 0,3	8,2 ± 1,8	6,0 ± 0,0	6,0 ± 0,0	6,0 ± 0,2	7,5 ± 1,3
<i>M. pruriens</i>	–	–	–	0,7 ± 3,1	–	–	–	66,0 ± 3,4

–: unavailable data, GRC: germination rate coefficient, SDG: starting day of germination.

in the optimum temperature range for each species, and this process started, in general, in less than eight days (tables 2 and 3). Of the plants with dormant seeds, 15 species (65,2 %, in relation with the total dormant-seed plants) –*G. sagreana*, *P. domingensis*, *B. cassinifolia*, *C. grandiflorum*, *A. dentata*,

M. glabra, *P. sexflora*, *P. suberosa*, *Dioscorea tamoides*, *D. rugosa*, *S. mollis*, *S. laurifolia*, *C. racemosa*, *A. precatorius* and *M. pruriens*– needed more than 28 days to start germination, and 7 (30,4 %) –*C. xalapensis*, *H. verticillata*, *I. suffruticosa*, *C. laurifolium*, *J. verticillata*, *R. reticulata* and *T.*

Table 4. Percentage of non germinated living seeds under different sowing conditions.

Species	Light				Darkness			
	25 °C	25/30 °C	25/35 °C	25/40 °C	25 °C	25/30 °C	25/35 °C	25/40 °C
<i>Shrubs</i>	0	0	0	0	0	0	0	0
<i>G. sagreana</i>								
<i>C. xalapensis</i>	90,8 ± 1,4	78,8 ± 1,9	73,6 ± 0,8	84,0 ± 2,2	96,0 ± 2,4	82,2 ± 0,9	96,0 ± 2,1	93,2 ± 2,9
<i>P. carolinensis</i>	80,4 ± 4,5	46,0 ± 0,0	4,2 ± 2,1	13,3 ± 3,8	93,2 ± 1,6	90,5 ± 0,7	43,0 ± 3,2	68,3 ± 1,8
<i>C. odorata</i>	35,0 ± 5,7	10,7 ± 0,5	30,5 ± 6,3	31,4 ± 7,1	85,0 ± 1,3	78,3 ± 3,1	81,8 ± 3,3	80,3 ± 1,3
<i>H. verticillata</i>	46,6 ± 0,6	30,4 ± 0,3	23,3 ± 1,6	28,6 ± 2,6	88,0 ± 4,6	63,3 ± 2,1	60,1 ± 3,1	50,8 ± 0,3
<i>S. jamaicense</i>	97,0 ± 1,5	22,7 ± 8,6	15,3 ± 12,3	15,5 ± 4,7	90,3 ± 2,1	84,8 ± 1,2	78,3 ± 2,1	63,6 ± 3,2
<i>S. torvum</i>	97,0 ± 1,0	0	3,3 ± 0,7	10,0 ± 5,0	93,2 ± 1,3	95,3 ± 2,1	37,3 ± 3,2	62,8 ± 1,8
<i>I. suffruticosa</i>	83,3 ± 1,3	80,4 ± 2,1	73,5 ± 1,0	30,3 ± 2,4	80,8 ± 12	79,3 ± 1,8	74,3 ± 3,1	70,6 ± 1,2
<i>C. laurifolium</i>	26,6 ± 4,8	26,6 ± 3,7	80,0 ± 0,8	33,3 ± 1,2	20,1 ± 3,1	30,2 ± 3,4	50,3 ± 3,1	50,3 ± 2,2
<i>P. domingensis</i>	0	0	0	0	0	0	0	0
<i>B. cassinifolia</i>	55,0 ± 3,3	52,3 ± 1,0	0	0	46,3 ± 1,2	34,3 ± 1,8	0	0
<i>C. grandiflorum</i>	25,0 ± 1,3	32,8 ± 2,6	0	0	32,7 ± 1,5	28,0 ± 3,2	0	0
<i>A. dentata</i>	0	0	0	0	0	0	0	0
<i>M. glabra</i>	0	0	0	0	0	0	0	0
<i>Climbing plants</i>								
<i>J. verticillata</i>	76,6 ± 8,8	55,0 ± 2,8	43,3 ± 3,3	38,3 ± 4,4	70,3 ± 2,8	80,6 ± 3,1	50,3 ± 1,8	48,0 ± 2,3
<i>P. sexflora</i>	90,0 ± 5,0	91,6 ± 1,6	21,3 ± 5,8	25,8 ± 7,4	93,0 ± 1,4	85,3 ± 2,3	13,8 ± 0,5	40,1 ± 2,8
<i>P. suberosa</i>	0	0	0	0	0	0	0	0
<i>G. lupuloides</i>	0	0	0	0	0	0	0	0
<i>D. tamoidea</i>	34,6 ± 2,2	21,3 ± 0,3	33,8 ± 1,3	23,1 ± 2,8	45,0 ± 3,8	20,3 ± 1,3	38,4 ± 2,3	28,0 ± 3,6
<i>L. divaricata</i>	0	0	0	0	0	0	0	0
<i>D. rugosa</i>	0	0	43,2 ± 3,8	48,4 ± 5,5	0	0	50,3 ± 4,1	56,3 ± 1,2
<i>R. reticulata</i>	83,4 ± 2,1	70,3 ± 3,8	50,4 ± 1,3	40,8 ± 2,1	80,1 ± 3,6	76,3 ± 1,2	48,3 ± 3,4	32,8 ± 1,2
<i>T. corymbosa</i>	95,0 ± 1,3	89,9 ± 1,9	76,6 ± 7,9	23,2 ± 5,8	90,3 ± 2,1	93,2 ± 3,4	83,1 ± 1,2	53,1 ± 4,0
<i>C. ternatea</i>	27,5 ± 10,9	17,5 ± 7,0	9,2 ± 3,2	0	30,3 ± 2,5	13,0 ± 1,6	12,6 ± 3,4	6,0 ± 1,3
<i>S. mollis</i>	72,3 ± 1,3	80,3 ± 2,3	90,5 ± 1,8	93,2 ± 3,6	70,3 ± 3,2	91,0 ± 1,3	87,3 ± 4,1	93,8 ± 2,1
<i>C. racemosa</i>	0	0	0	0	0	0	0	0
<i>S. laurifolia</i>	83,0 ± 0,6	91,0 ± 3,4	96,0 ± 3,8	83,0 ± 1,5	73,4 ± 1,3	85,3 ± 2,4	90,4 ± 1,7	80,3 ± 2,1
<i>A. precatorius</i>	95,0 ± 0,0	98,3 ± 1,6	23,3 ± 8,8	10,0 ± 5,0	89,3 ± 1,8	93,6 ± 1,3	33,2 ± 0,3	20,3 ± 1,4
<i>B. glabra</i>	0	0	0	0	0	0	0	0
<i>M. pruriens</i>	100	100	100	87,0 ± 0,5	100	90,0 ± 1,3	93,0 ± 2,5	85,0 ± 1,3

corymbosa– finished the experiment with more than 20 % of non-germinated living seeds. The seeds from *D. tamoidea*, *S. mollis* and *S. laurifolia* showed underdeveloped embryos, and the *L. divaricata* seeds reached their maximum germination (27,7 %) in a temperature range (25/35 °C) which did not exist in the soil when they were dispersed, for which they were considered dormant.

The imbibitions tests of 9 species with primary dormancy showed that the seeds of all of them, except *I. suffruticosa* and *M. pruriens*, were hydrated after they spent 24 h in contact with the water (table 5). Nevertheless, the cutting tests of fresh seeds of *J. verticillata*, *R. reticulata*, *T. corymbosa* and *A. precatorius* showed that at least 30, 40, 20 and 10 %, respectively, were not hydrated at the end of the germination experiment.

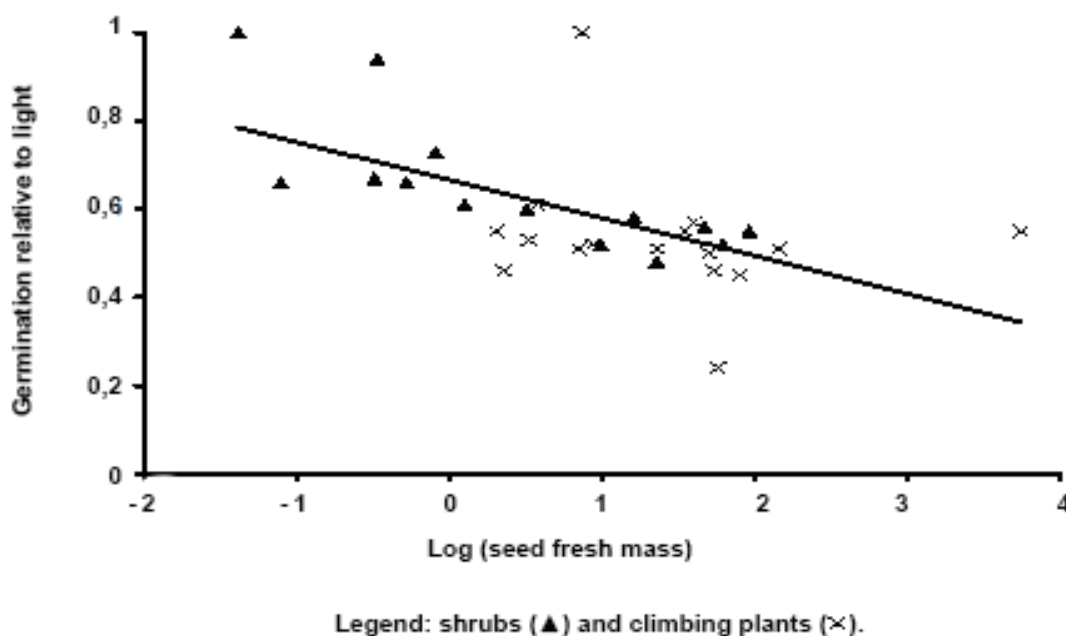


Figure 2. Linear relation between the seed mass and the germination relative to light.

Table 5. Water content of the seeds with primary dormancy.

Species	Imbibition time (hours)				<i>F</i> -test ^a
	0 ^a	24	48	72	
<i>A. dentata</i>	14,13 ± 1,3	19,3 ± 0,8	24,6 ± 1,9	35,8 ± 1,5	***
<i>A. precatorius</i>	7,46 ± 0,9	34,7 ± 1,5	46,2 ± 3,2	51,2 ± 1,6	***
<i>B. cassinifolia</i>	29,21 ± 0,8	32,4 ± 2,3	38,5 ± 1,8	41,0 ± 2,1	***
<i>C. grandiflorum</i>	9,11 ± 0,8	16,9 ± 0,6	26,9 ± 1,5	30,3 ± 1,8	***
<i>I. suffruticosa</i>	12,5 ± 1,0	12,9 ± 0,9	13,5 ± 0,9	13,6 ± 1,3	NS
<i>J. verticillata</i>	24,39 ± 1,4	32,5 ± 1,6	39,8 ± 0,6	44,3 ± 3,1	***
<i>M. pruriens</i>	4,63 ± 0,4	4,68 ± 0,8	4,56 ± 0,3	4,78 ± 0,9	NS
<i>R. reticulata</i>	10,43 ± 1,5	14,6 ± 1,0	18,9 ± 1,9	23,1 ± 2,3	**
<i>T. corymbosa</i>	8,72 ± 2,3	15,9 ± 1,7	29,7 ± 2,4	34,9 ± 2,0	***

^aInitial water content of the seeds (%).

^aDifferences according to the ANOVA. NS: non-significant; **: $p < 0,01$; ***: $p < 0,001$.

The TMS treatment was effective to increase the FG percentage in 3 of the 4 species that were tested (table 6); although in *C. laurifolium* the FG increased, but the germination rate did not rise. In the *A. dentata* seeds this pre-germination treatment was not effective, and in fresh *M. pruriens* seeds the testa rupture increased and accelerated germination.

It can be summarized that 14 species showed physiological dormancy as the only impediment

for their germination; 6, physical dormancy (in at least a fraction of the lot seeds), and 3, morphological and morpho-physiological dormancy. No species with combination of dormancy was identified. In the shrubs the PD prevailed (9 species) and in the climbing plants PD and PY were equitably distributed, that is, 5 species showed PD and 5, PY. In the climbing plants the only species with underdeveloped embryos and, thus, with MD +MPD or MPD were also found.

Life history traits per dormancy classes. The final germination percentage (FG) and the starting day of germination (SDG) showed significant variability according to the dormancy classes (table 7). The seeds with morphological and/or morpho-physiological dormancy showed the lowest FG and the highest SDG values, and the non dormant seeds had the highest FG and the lowest SDG. For the other seed traits studied no significant differences were detected per dormancy class, possibly due to the large variability they showed.

On the other hand, the percentage of species with dormant seeds varied with the dispersal time (table 8). The seeds from 15, 13 and 2 species were collected during the DS, ERS and LRS, respectively. The species dispersed in the DS showed more dormant seeds (87 %, with regards to the total collected in the season) than those collected in the ERS (77 %), and the ones collected in the LRS did not

have dormant seeds. Most of the species dispersed in the ERS and the DS showed PD (38,4 and 60,0 %, respectively) and from the 6 species with PY, 4 were found in the DS. From the 15 species that were dispersed by the animals, 13 had dormancy (86,6 %): 11 with PD (73,3 %) and 2 with MD or MPD (13,3 %). On the contrary, in the ones not dispersed by the animals, dormancy was present in 10 species out of 15, and physical dormancy prevailed (40 %).

DISCUSSION

The temperature and substratum light affected germination in all the species (per community), and the light was the main factor that regulated such process. According to Pons (2000) and Pearson *et al.* (2002), in the forest canopy, the main limiting factor of germination is usually the light that reaches the soil, because it decreases in quantity and quality due to the vegetation. Such result was more

Table 6. Effect of pre-germination treatments on the germination of species with primary dormancy.

Species	Treatment	Final germination (%)		Start of germination (days)	
		Control	Treatment	Control	Treatment
<i>A. dentata</i>	TMS	2,6 ± 3,1	28,3 ± 1,8 NS	35,3 ± 2,3	33,33 ± 1,2 NS
<i>B. cassiniifolia</i>	TMS	27,7 ± 3,5	92,1 ± 5,5***	70,0 ± 7,5	17,0 ± 0,2***
<i>C. grandiflorum</i>	TMS	33,3 ± 6,9	100***	45,0 ± 0,5	4,7 ± 0,3***
<i>C. laurifolium</i>	TMS	50,6 ± 2,3	73,5 ± 1,2**	13,0 ± 2,1	14,1 ± 0,6 NS
<i>M. pruriens</i>	TR	11,2 ± 2,3	100***	66,0 ± 3,4	7,3 ± 1,3***

NS: not significant; **: $p < 0,01$; ***: $p < 0,001$;

TMS: total mechanical scarification; TR: testa rupture.

Table 7. Mean values (± SE) of history traits per seed dormancy classes.

Variables ¹	ND ² (n = 7)	PD (n = 14)	MD + MPD (n = 3)	PY (n = 6)	R-ANOSIM ³
SFM	28,7 ± 20,6	19,8 ± 5,9	46,6 ± 21,0	946,6,5 ± 911	0,02 NS
WC	15,6 ± 4,4	15,2 ± 1,6	20,1 ± 3,1	11,4 ± 2,8	0,12 NS
DMC	52,8 ± 5,4	39,0 ± 5,5	24,5 ± 11,8	35,2 ± 6,4	0,02 NS
GRL	0,64 ± 0,06	0,60 ± 0,05	0,47 ± 0,02	0,55 ± 0,01	-0,06 NS
FG	85,9 ± 3,3	40,5 ± 4,1	35,9 ± 16,0	48,3 ± 10,5	0,48 ***
SDG	7,9 ± 2,3	38,1 ± 6,4	50,9 ± 11,6	23,8 ± 8,9	0,28***

¹SFM, seed fresh mass (mg); WC, water content (%); DMC, dry matter percentage of the seed coat; GRL, index of germination relative to light; FG, germination percentage; SDG, starting day of germination.

²ND: non-dormant; PD: physiological dormancy; MD + MPD: morphological and morpho-physiological dormancy, PY: physical dormancy. n = number of species.

³NS: not significant; ***, $P \leq 0.001$.

Table 8. Dispersal time, form of dispersal and seed dormancy classes.

Species	Dispersal time ¹	Dispersal form ²	Dormancy class
Shrubs			
<i>G. sagreana</i>	DS	ZOO	PD
<i>C. xalapensis</i>	ERS	ZOO	PD
<i>P. carolinensis</i>	ERS	NO ZOO	ND
<i>C. odorata</i>	ERS	NO ZOO	ND
<i>H. verticillata</i>	DS	NO ZOO	PD
<i>S. jamaicense</i>	ERS	ZOO	ND
<i>S. torvum</i>	LRS	ZOO	ND
<i>I. suffruticosa</i>	ERS	NO ZOO	PY
<i>C. laurifolium</i>	ERS	ZOO	PD
<i>P. domingensis</i>	DS	ZOO	PD
<i>B. cassinifolia</i>	ERS	ZOO	PD
<i>C. grandiflorum</i>	DS	ZOO	PD
<i>A. dentata</i>	DS	ZOO	PD
<i>M. glabra</i>	DS	ZOO	PD
Climbing plants			
<i>J. verticillata</i>	ERS	NO ZOO	PY
<i>P. sexflora</i>	DS	ZOO	PD
<i>P. suberosa</i>	ERS	ZOO	PD
<i>G. lupuloides</i>	DS	NO ZOO	ND
<i>D. tamoidea</i>	ERS	NO ZOO	MPD
<i>L. divaricata</i>	DS	NO ZOO	PD
<i>D. rugosa</i>	ERS	NO ZOO	PD
<i>R. reticulata</i>	DS	NO ZOO	PY
<i>T. corymbosa</i>	DS	NO ZOO	PY
<i>C. ternatea</i>	LRS	NO ZOO	ND
<i>S. mollis</i>	ERS	ZOO	MPD
<i>C. racemosa</i>	DS	ZOO	PD
<i>S. laurifolia</i>	ERS	ZOO	MPD
<i>A. precatorius</i>	DS	NO ZOO	PY
<i>B. glabra</i>	DS	NO ZOO	ND
<i>M. pruriens</i>	DS	NO ZOO	PY

¹DS, dry season; ERS, early rainy season; LRS, late rainy season.²ZOO, dispersal by animals and NO ZOO, not dispersed by animals.

evident when germination was analyzed per life form. In most shrubs, this variable was stimulated by light, mainly in the range of 25/30 °C, but also at 25/35 °C and 25/40 °C. This performance has been reported for a large number of pioneer tree spe-

cies of the Neotropics (Vázquez-Yanes and Orozco-Segovia, 1994; Pearson *et al.*, 2002), as well as in Cuba, for this same ecological group of the studied area (Sánchez *et al.*, 2003; Muñoz *et al.*, 2012). The observations in the collection site proved that

many of the shrub seedlings were found indistinctly in open or semi-open sites.

The germination response of the shrubs in the essayed temperature ranges showed that the germination was also conditioned by the temperature alternance of the substratum, as occurs in forest clearings (Vázquez-Yanes and Orozco-Segovia, 1994). In fact, the large majority of shrubs (studied or not in the germination tests; Sánchez, J. A., unpublished) dispersed their seeds during the early rainy season—or summer season for Cuba— (48,8 %); for which it was proven that this is conditioned by a spatial (open vegetation structure) and weather variability (concentration of rainfall and temperature increase), probably to maximize the establishment and survival of the individuals (Baskin and Baskin, 1998).

A large interspecific variability with regards to temperature was observed in the climbing plants, for which no germination preference was detected for a particular temperature range (fig. 1C); although it is necessary to state that in the species with PY (*I. suffruticosa*, *J. verticillata*, *R. reticulata*, *T. corymbosa*, *A. precatorious* and *M. pruriens*) the best germination response was obtained at 25/40 °C (table 2). The conditions of complete darkness significantly increased germination in four climbing plants (*P. sexflora*, *S. mollis*, *S. laurifolia* and *C. racemosa*); the better response in *S. mollis* and *S. laurifolia* at 25 °C and under darkness conditions showed the adaptation of these taxa to germinate deep in the forest, where the air temperature remains relatively constant during almost the whole year -25 ± 2 °C— (Herrera *et al.*, 1988) and the light that reaches the soil is poor in red and rich in far-red (Vázquez-Yanes and Orozco-Segovia, 1990). From these four species, the only one that tended to be negative photoblastic was *C. racemosa*, because it reached the lowest GRL values (0,24). Probably this performance is normal, because this plant grows in semi-closed sites of the forest; however, its best germination response at 25/30 °C does not fully support this hypothesis.

The germination response of the fresh seeds of climbing plants showed high plasticity, because no marked germination preference for the tested factors was shown. Sanches and Válio (2002) also found a similar result in 13 climbing plants, in a tropical forest of Brazil, which germinated and were established in clearings, in semi-shaded sites or in the forest depths.

Through all the species it was shown that light, as signal for germination, was less important in those with large seeds than in the ones which had small seeds (fig. 2). This pattern was detected for the first time, at community level, by Grime *et al.* (1981) in plants from temperate regions. Milberg, Andersson and Thompson (2000) observed a similar performance in 54 herbaceous species, with or without phylogenetic control, for which they concluded that the light requirements for germination have co-evolved with the seed mass.

Recently Flores *et al.* (2011) obtained, in seeds of cacti from seven countries, a negative relation between the GRL index and the seed mass; this coincides with the results obtained by Sánchez *et al.* (2012) in 60 trees belonging to the studied site. It is important to state that the determination coefficient (R^2) between the index of germination in the light and the logarithm of the seed fresh mass in this study was low ($R^2 = 0,339$), and similar to the one found by Milberg, Andersson and Thompson (2000) $-R^2 = 0,277-$ and Sánchez *et al.* (2012) $-R^2 = 0,280-$, which showed that in both floras the germination response to the light varied greatly, and not all the variation was due to the seed mass. In fact, this variable only explained 33 % of the variation of the GRL index. Several authors have stated that photosensitivity is a complex phenomenon, in which intrinsic traits of each seed and their relation to the edaphoclimatic environment are involved (Baskin and Baskin, 1998; Pons, 2000).

In the small group of shrubs and climbing plants a high percentage of species with dormant seeds was found, in the dry season (87 %) as well as in the early rainy season (77 %), which exceeds the dormancy values reported for these life forms in the seasonal moist forests of the tropics (Baskin and Baskin, 1998). In fact, the little existing information on the dormancy of climbing plants and shrubs indicates that most of these species show non dormant seeds when they occupy humid sites, and in the case they are dormant, in climbing plants PD, PY and MPD prevail, and in shrubs, PD and PY (Baskin and Baskin, 1998). Nevertheless, from the 14 shrubs, 10 species showed dormancy (71,4 %); with predominance of the physiological class. According to Baskin and Baskin (1998), this dormancy class is the most frequent for all vegetation types and life forms (trees, shrubs, vines and grasses) of the tropical and subtropical zones of the world. It has also been reported that it is the most impor-

tant one for all the angiosperm clades (Baskin and Baskin, 2003; Silveira *et al.*, 2012).

This result contrasts with the theoretical models which have been proposed at global scale, and which presuppose that the number of species with germination delaying strategies (i.e., seed dormancy) increases in unfavorable environments with regards to those that occupy favorable habitats (Jurado and Moles, 2003; Baskin and Baskin, 2005; Jurado and Flores, 2005); although it is also known that these studies do not allow to conclude accurately about the processes that are involved in the assembling (or species matrix) of the local communities (Bu *et al.*, 2008; Kos, Baskin and Baskin, 2012). In fact, many of the species that disperse their seeds in the so-called optimum growth season (ERS) of these seasonal forests have seed dormancy (Sautu *et al.*, 2007; Sánchez *et al.*, 2012); thus, dormancy does not seem to be, in this season, a delaying strategy to wait for the arrival of more adequate environmental conditions (increase of temperature and rainfall) to germinate. It rather seems to be a strategy to prevent the predation of the cohort of seedlings, although it could also avoid drought processes within the rainy season. The effect of this last ecological scenario on the seedling mortality in the moist forests of the SRBR was documented by Herrera *et al.* (1988), and by Engelbrecht *et al.* (2006) for pioneer species of forests in Panama.

The results also showed that the seeds of the climbing plants had higher delay to start germination with regards to those of shrubs, which is maybe due to the fact that the former showed the highest number of species with PY and the only three species with MD and/or MPD (Baskin and Baskin, 2004). Likewise, most of these species were dispersed during the dry season; thus, the dormancy of this group of plants could be a delaying strategy until the arrival of the optimum conditions to germinate and establish the seedlings (Jurado and Morales, 2003; Salazar *et al.*, 2011). This germination response is in correspondence with the germination syndrome found by Garwood (1983) and Sautu *et al.* (2007) for the tree species of the seasonal forests of Panama and for the trees of the studied site (Sánchez *et al.*, 2012).

According to the results of the imbibition, cut and germination tests, it was confirmed that the fresh seeds of *A. precatorius*, *I. suffruticosa*, *J. verticillata*, *M. pruriens*, *R. reticulata* and *T. corymbosa* showed PY as the main obstacle for germination, as has been previously reported for

families of these species –*Fabaceae* and *Convolvulaceae*– (Baskin, Baskin and Li, 2000; Gehan *et al.*, 2012) and for some of the studied species (Brancalion *et al.*, 2010).

In the intact seeds of *A. precatorius*, *M. pruriens*, *R. reticulata* and *T. corymbosa* the highest FG percentages were obtained at alternate temperatures of 25/40 °C and 25/35 °C. However, these temperatures are not the ones found by the seeds when they fall to the soil in the dry season (winter for Cuba), because such ranges can only be reached in the rainy season. Thus, it was evident that the hot scarification accelerated the rupture of the dormancy of, at least, a portion of the seeds; this treatment is widely acknowledged to eliminate PY (Baskin and Baskin, 2004). In *M. pruriens* seeds, with the treatment of testa rupture and sowing at 25/40 °C germination could be increased up to 100 %, result which was also obtained for this species at 25/30 °C and 25/35 °C (data not shown) and coincides with the statement by Baskin and Baskin (1998) regarding the wide germination capacity shown by the seeds with PY after they are subject to scarification. The *A. precatorius* seeds showed the best germination response when the substratum temperature increased, and achieved 90 % of FG at 25/40 °C. However, at constant temperature of 25 °C and at 25/30 °C more than 90 % of them were not hydrated at the end of the experiment. This species shows simulated mimicry and the PY allows it to survive the deterioration undergone by the seeds during their passage through the digestive tract of dispersers (Brancalion *et al.*, 2010). Nevertheless, its primary dispersal mechanism is autochory, thus, the PY could also be useful for it to remain viable in the soil.

In the seeds of *I. suffruticosa* (*Fabaceae*) and *J. verticillata* (*Convolvulaceae*), the germination percentages that were reached at 25/40 °C were not so high (35 and 60 %, respectively); thus, there was an important fraction of the lot which seemingly had a higher depth of PY, possibly as a mechanism to extend germination during the rains, because the seeds reached the soil in the early rainy season (April). However, the proposed mechanism might not work for *I. suffruticosa*, because the species is not native from the SRBR.

The imbibition tests indicated that PY did not constitute the main obstacle for germination in the seeds of *A. dentata*, *B. cassiniifolia* and *C. grandiflorum*. In the seeds of these species the presence of underdeveloped embryos has not been reported ei-

ther (Montejo *et al.*, 2014b), for which it is assumed that they did not show MD or MPD or the combination of any of them with PY; then, they can only have PD, which is the most common dormancy in some of these families (Baskin and Baskin, 1998). A similar analysis can be made for the seeds of *G. sagreana*, *C. xalapensis*, *H. verticillata*, *C. laurifolium*, *P. domingensis*, *M. glabra*, *P. sexflora*, *P. suberosa*, *L. divaricata*, *D. rugosa* and *C. racemosa*, although no imbibition tests were made. In the families of these species the embryos are developed and PY has never been reported, except in *C. racemosa* –*Cucurbitaceae*– (Baskin, Baskin and Li, 2000); however, their seeds were hydrated since the beginning of the germination tests. It has also been suggested that there could be PY in *Passifloraceae* due to the anatomy of their coats (Baskin, Baskin and Li, 2000), but the seeds of *P. sexflora* and *P. suberosa* were very rapidly hydrated; thus, for these last 11 species it is equally assumed that they showed PD, which is due to mechanisms of physiological inhibition in the embryo (Baskin and Baskin, 1998).

The fresh seeds of Cuban endemic shrubs (*A. dentata*, *C. grandiflorum* and *G. sagreana*) reached the soil in the dry season and showed PD, as it was commented above; however, the depth of this dormancy changed with the species. The *C. grandiflorum* seeds increased and significantly accelerated the final germination with the TMS; which suggests that they must have non-deep PD, as is reported for the family *Verbenaceae* (Baskin and Baskin, 1998). According to Baskin and Baskin (2004), the pre-germination TMS treatment is adequate to eliminate this type of dormancy. Nevertheless, it was not effective on *A. dentata*: a fraction of the seed lot (30 %) should have shown non-deep PD because they germinated after 28 days, and the other fraction which did not germinate (70 %) even with the pre-germination treatment is likely to have shown intermediate or deep PD. These *A. dentata* seeds reach the soil in the late dry season (March) and are ingested by the animals, for which it is very probable that the PD allows them to survive until the start of the rainy season, or rather during their passage through the digestive tract, as has been reported for a large number of species which are dispersed by animals (Bu *et al.*, 2008).

The *G. sagreana* seeds started germination after 36 days and did not reach more than 50 % of final germination at the optimum temperature (25/30 °C), for which they showed PD, as has been report-

ed for the family *Rubiaceae* (Baskin and Baskin, 1998). The results also proved that at least a fraction of the lot (50 %) should have shown intermediate or very deep PD, because 80 days after their sowing that fraction had not germinated yet. This portion of seeds probably remains viable in the soil until the rains start, but maybe they could form a more stable seed bank, because they were the smallest (0,042 mg), positive photoblastic, and destined more than 40 % of their dry mass to the physical defense structures (testa/endocarp); morpho-physiological traits which allow to form a seed bank (Thompson *et al.*, 2003) and, thus, respond to disturbances. These characteristics appear in early pioneer tree species of Cuban forests (Muñoz *et al.*, 2012). In fact, *G. sagreana* is considered an expansive native plant (Ricardo and Herrera, 2010).

On the other hand, the seeds of *H. verticillata* and *L. divaricata* germinated in less than 28 days, but reached their maximum final germination (70,6 and 27,7 %, respectively) in a temperature range that they do not find when they reach the soil (25/35 °C), during the dry season; thus, this range accelerated the post-maturation of at least a fraction of the lot. Seemingly the PD was deeper in the second species, because germination was very low. The *L. divaricata* seeds were also positive photoblastic, which suggests that they could remain viable in the soil for a while, as was previously discussed for *G. sagreana*. The fresh seeds of *C. xalapensis* (*Melastomataceae*) and *C. laurifolium* (*Solanaceae*) also germinated in less than 28 days, but left a high percentage of dormant seeds in the best sowing temperature (73,6 and 26,6 %); for which at least those fractions showed PD, which is the reported dormancy in their families (Baskin and Baskin, 1998; Silveira *et al.*, 2012). Probably, the PD in these species is a mechanism to survive the digestive tract of their dispersers (birds and bats), because they reach the soil in the full rainy season (May). The PD in at least one fraction of the *C. laurifolium* seeds seems to be of the intermediate type, because the TMS only was effective on one fraction of the lot (23 %) and did not accelerate germination either; likewise, the pre-germination treatment with giberelic acid did not promote germination (Sánchez, J. A., unpublished) more than the TMS used did.

The seeds of *B. cassinifolia*, *P. sexflora*, *P. suberosa*, *M. glabra*, *P. domingensis* and *D. rugosa* needed more than 28 days to start germination (between 39,3 and 97,3 days), showed developed embryos and were permeable to water, for which there

are no doubts that they showed PD. All of them, except *D. rugosa*, are dispersed by the animals and reach the soil in the dry season, which justifies the PD. In the *B. cassiniifolia* seeds the pre-germination treatment was effective to improve germination and for such reason they showed non-deep PD, although they reached the soil in the early rainy season. Some tree species of *Psychotria* (*Rubiaceae*) are described as dormant (Garwood, 1983; Baskin and Baskin, 1998; Sánchez *et al.*, 2012). Seemingly, 38,3 % of the *P. domingensis* seeds had non-deep PD, but for the others there was not sufficient evidence that allowed to determine the level of PD. This situation was similar for *P. sexiflora*, *P. suberosa* and *M. glabra*.

Finally, the seeds of *D. tamoidea*, *S. mollis* and *S. laurifolia* showed underdeveloped embryos and thus MD or MPD dormancy, as have been reported for the families *Smilacaceae* and *Discoriaceae* (Baskin and Baskin, 1998). An important fraction of the *D. tamoidea* seeds (67,8 %) started germination after 30 days (35,7 days); consequently, such fraction should have shown MD, although 60 days after sowing more than 20 % remained alive without germinating, which suggests that at least that percentage of seeds had MPD. The seeds of *S. mollis* and *S. laurifolia* showed MPD, because germination started after 40 days and more than 70 % did not germinate. The other studied liana (*C. racemosa*) also showed dormancy, but of physiological class, probably non-deep, because it reached 100 % of germination in the darkness, and under these conditions germination started at 32 days (data not shown). Dormancy in this life form seems to be pretty common, as the two non-studied species of lianas (*Forteronia corymbosa* and *Smilax havanensis*) belong to families with dormancy (Baskin and Baskin, 1998). Also Gehan *et al.* (2012) found PD and PY in tropical lianas of the family *Fabaceae*.

FINAL CONSIDERATIONS

The results showed that the abiotic factors (light and temperature) considerably affected the

germination of the shrub species. In the climbing plants, when the germination response was wholly analyzed, none of the studied factors significantly influenced this variable, which suggests that these plants can occupy many microsites; however, for some of them a species-specific response appears. On the other hand, the response to the temperature range of 25/40 °C proved that many of the shrub species can be very sensitive to the increase of the air temperature, as is proposed in the possible scenarios of the climate change (IPCC, 2007), which in the case of Cuba is estimated to vary between 1,6 and 2,5 °C in 2100 (Capote, Mitrani and Suárez, 2011). Therefore, the climate change could alter the composition and structure of the vegetation and, thus, induce a progressive substitution of the dormancy classes that compose the species of the plant community, that is, those species with physical dormancy would be favored. Nevertheless, according to the results, this type of dormancy is not very common in the shrubs that are included in this forest formation, for which the water and heat stress (drought) could favor another kind of strategy to ensure the establishment of the community—for example, the increase of non-dormant species, or species with deep physiological dormancy—or rather to benefit those species with high proportions of resources destined to the testa/endocarp defense structures (Garwood, 1983; Salazar *et al.*, 2011).

ACKNOWLEDGEMENTS

This study was funded by the International Foundation for Science through the donation D/3536-2 given to J. A. Sánchez. In addition, the studies were conducted within the framework of the project “Ecophysiology of tree and shrub seeds and seedlings of Sierra del Rosario”, of the Program of Biological Diversity of Cuba.

Received: December 16, 2013

Accepted: December 2, 2014