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**LIGHT AND TEMPERATURE REQUIREMENTS FOR GERMINATION OF SEEDS OF
AECHMEA NUDICAULIS (L.) GRIESEBACH AND *STREPTOCALYX FLORIBUNDUS*
(MARTIUS EX SCHULTES F.) MEZ (BROMELIACEAE)**

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RESUMO – [Requerimentos de luz e temperatura para a germinação de sementes de *Aechmea nudicaulis* (L.) Griesebach e *Streptocalyx floribundus* (Martius ex Schultes F.) Mez (Bromeliaceae)]. Sementes de *A. nudicaulis* e *S. floribundus* foram coletadas em uma restinga em Presidente Kennedy (ES). Esta comunidade arenosa caracteriza-se pela presença de moitas de vegetação separadas por areia nua ou com rala cobertura vegetal. Para examinar a capacidade das sementes em germinar nas distintas situações microclimáticas presentes neste ambiente, foram conduzidos, em laboratório, experimentos de germinação sob diferentes condições de temperatura e luminosidade. Sementes de *A. nudicaulis* não germinaram no escuro, mas sob luz vermelha atingiram alta germinabilidade ($\geq 90\%$) entre 15 e 40°C. Sementes de *S. floribundus* germinaram no escuro apenas a 40°C (22,5%), enquanto na luz, a germinabilidade foi acima de 90% entre 15 e 30°C. Para ambas as espécies a velocidade de germinação foi máxima a 25°C. Para as duas bromélias, temperaturas alternantes (20/30°C) resultaram em alta germinabilidade ($\geq 92,5\%$) apenas na luz. Sementes mantidas a 20/30°C no escuro foram posteriormente transferidas para luz, resultando numa alta germinabilidade ($> 89\%$) para ambas as espécies. Nenhuma semente germinou a 20/50°C, perdendo a viabilidade após 720h de incubação. As sementes mostraram-se fotoblásticas positivas e não toleraram altas temperaturas. Em condições naturais, a germinação de *A. nudicaulis* e *S. floribundus* parece ser dependente da presença de luz e de cobertura vegetal, sendo limitada em condições de soterramento e em sítios que apresentam temperaturas do solo elevadas.

Palavras-chave – *Aechmea nudicaulis*, *Streptocalyx floribundus*, restinga, germinação, temperatura

ABSTRACT – [Light and temperature requirements for germination of seeds of *Aechmea nudicaulis* (L.) Griesebach and *Streptocalyx floribundus* (Martius ex Schultes F.) Mez (Bromeliaceae)]. Seeds of *A. nudicaulis* and *S. floribundus* were collected in a restinga located at Presidente Kennedy (ES, Brazil). This sandy community is characterized by the presence of patches of vegetation interspersed by open areas with a sparse plant covering. In order to evaluate the capacity of *A. nudicaulis* and *S. floribundus* to recruit individuals from seeds in the distinct microclimates generated by this heterogeneous plant covering, experiments were conducted in laboratory to test the effects of light and temperature on the germination for both species. Seeds of *A. nudicaulis* were unable to germinate in darkness but they achieved high germinability ($\geq 90\%$) from 15 to 40°C under red light. Seeds of *S. floribundus* germinated in darkness only at 40°C (22.5%), whereas the germinability was high ($\geq 90\%$) from 15 to 30°C under

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light. For both species, the germination rate was highest at 25°C. For these bromeliads, alternating temperature (20/30°C) promoted high germinability ($\geq 92.5\%$) only under red light. The seeds at 20/30°C in darkness were later transferred to light and a high germinability ($>89\%$) was achieved for both species. No seed germinated at alternating temperatures of 20/50°C and they were dead after 720h of incubation. The seeds showed to be photoblastic and did not tolerate high temperatures. The results suggest that under natural conditions the germination of seeds of *A. nudicaulis* and *S. floribundus* is restricted to microclimates where light and moderate temperatures are present. The microsites generated by the plant covering seem to provide these requirements.

Key words – *Aechmea nudicaulis*, *Streptocalyx floribundus*, restinga, seed germination, temperature

Introduction

The sandy coastal plain (Restinga) along the Brazilian coastal line has a great diversity of plant communities which species composition and spatial plant distribution result from topographic peculiarities and distinct environmental conditions (Araújo & Henriques 1984; Henriques *et al.* 1986). Some of those formations (*Clusia* and Ericaceae formation) are characterized by the scattered occurrence of patches of vegetation consisting of cacti, bromeliads, shrubs and trees, interspersed by open areas where a sparse vegetation constituted by bromeliads, palms and small shrubs is present (Henriques *et al.* 1986). High temperatures achieved by soils exposed to full sun (Franco *et al.* 1984; 1996), water stress and oligotrophism (Reinert *et al.* 1996) are among the limiting factors for the establishment of species in this community.

It has been found that some plants make possible the establishment of other species due to the shade provided by their canopy (Franco & Nobel 1988, 1989, Fulbright *et al.* 1995; Barnes & Archer 1996). These “nurse plants” reduce the soil desiccation by solar radiation and provide water availability for the associated seedlings. Maximum soil surface temperatures are also reduced by shading, thus furnishing an appropriate microhabitat for seed germination and seedling establishment beneath the canopy (Franco & Nobel 1988; 1989). This shading effect could be remarkably important in Restinga communities; Fialho (1990) reported a high mortality among seeds of *Erythroxylum ovalifolium* that fall on the sandy soil due to

extreme temperatures. Indeed, *Clusia* sp. (Zaluar 1997) and *Neoregelia cruenta* (Hay & Lacerda 1980) were shown to reduce maximum soil temperatures and to increase soil nutrients and organic matter, respectively.

It is well established that an understanding of vegetation dynamics requires a combination of intensive field studies (phenology, mortality, seed bank) and experimental approaches (Schat & Scholten 1985). Accordingly, several reports have correlated spatial and temporal dynamics of species in the field to dormancy status and germination characteristics of the seeds (Fenner 1980; Meyer *et al.* 1989; Maunn 1994; Fulbright *et al.* 1995; Meyer *et al.* 1995; Schupp 1995). Unfortunately, few studies on seed germination have been conducted for species of Restinga (e.g. Dau & Labouriau 1974; Mercier & Guerreiro Filho 1990; Fialho & Furtado 1993).

The bromeliads *Aechmea nudicaulis* (L.) Griesbach and *Streptocalyx floribundus* (Martius ex Schultes F.) Mez are conspicuous components of Restinga communities. Individuals of *A. nudicaulis* usually occur bordering the patches of vegetation (Dau 1960; Pereira 1990). In the Restinga where the seeds were collected for the present investigation, both species were frequently found at the edges of the thickets, and a few individuals were also found in open areas (F. Borghetti, pers. obs.). In view of these observations, we ask the following: would these species tolerate the high soil temperatures of open areas, thus acting as early colonizers in patch dynamics? Considering the effects of light and temperature on seed germination we discuss these possibilities for *A. nudicaulis* and *S. floribundus*.

Material and methods

Aechmea nudicaulis (L.) Griesebach occurs as epiphytic, rupestrine or terrestrial species, being described for several ecosystems including the sandy coastal plains of Brazil. *Streptocalyx floribundus* (Martius ex Schultes F.) Mez occurs as epiphytic or terrestrial species and can be found in coastal rain forests and sandy coastal plains of southeastern Brazil (Fontoura *et al.* 1991).

The seeds were collected in September 1996 in a Restinga located at "Barra de Itabapuana" (21°16' S and 40°48' W), municipality of Presidente Kennedy, southern coast of Espírito Santo State, southeastern Brazil. Warm and rainy summers and dry winters characterize the climate (Fig. 1). The distribution of the vegetation at that site is characterized by the occurrence of thickets interspersed by areas with a sparse plant cover. Temperature measurements of the soil surface were done daily during a week, using maximum-minimum thermometers (MM5201 Incoterm) installed under shaded microhabitats (inside thickets) and in soil exposed to full sunlight. The

thermometers were placed a few millimeters underground and covered with sand. The temperatures employed in the experiments described below were based on these field data.

In order to obtain representative seed samples of the local populations, several mature fruits were collected from at least 15 individuals of each species. In the laboratory, the seeds were removed from the fruits, dried at room temperature and stored at $22 \pm 2^\circ\text{C}$ in a dark room for about a month until use. Seed viability ($n = 100$) was estimated using a 0.5% tetrazolium salt solution (Copeland 1976). Seed germination studies were performed using incubators regulated at the following constant temperatures: 15, 20, 25, 30, 35, 40, 45°C (Precision Scientific Model 818, $T \pm 0.5^\circ\text{C}$). Alternating temperature treatments were 20/30°C and 20/50°C (16/8 h, respectively). The temperature treatments were applied under continuous red light and in darkness. Red light was produced by two fluorescent light sources with an appropriate optical filter. The fluence rate ($200 \mu\text{W}\cdot\text{cm}^{-2}$) was measured with an Eppley Thermopile and the spectra transmitted through the filter (610-695nm) was examined in

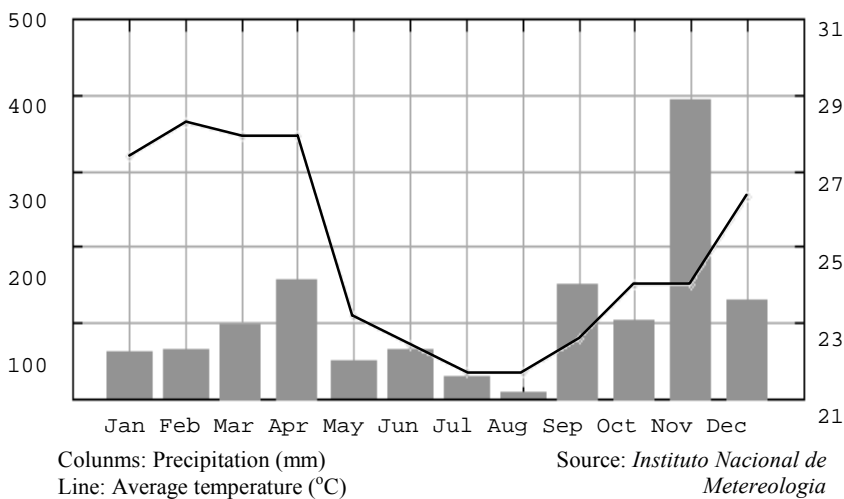


Figure 1. Average temperature ($^\circ\text{C}$) and precipitation (mm) recorded in 1996 for the municipality of Vitória (ES). Source: Instituto Nacional de Meteorologia.

a Gaertner L-205 spectroscope (Borghetti 1992). This wavelength range is the most effective in promoting the germination of light-requiring seeds (Bewley & Black 1994). Four replicates of 50 seeds were used for each treatment. The seeds were placed in 9cm Petri dishes with one layer of qualitative filter paper. At 24h intervals the germinated seeds were counted and removed. The observations were made under red light and deionized water was added as needed. For experiments conducted in darkness, the dishes were placed into black boxes in the beginning of the experiment and the observations were made under a green safelight (490-560nm) (Silveira & Labouriau 1995). The non-germinated seeds incubated at 20/30°C in darkness were transferred to red light after 240 h of incubation. Viability of the non-germinated seeds was evaluated at the end of the experiments using the tetrazolium solution.

Germinability (G = percentage of germinated seeds), the average germination time (t) and its variance (tS^2), and the average germination rate

(V = inverse of the average germination time) and its variance (vS^2) were computed according to Labouriau (1972). The distributions of seed germination at different temperatures were tested for their normality through the Kolmogorov-Smirnov test (Sokal & Rohlf 1995). Comparisons between average germination rates were performed through the Mann-Whitney U-test (Sokal & Rohlf 1995). Confidence intervals for germinabilities were obtained from *Tablas Cientificas* (Documenta Geigy 1965). All statistics used an a level of 0.05.

Results

The tetrazolium test indicated a seed viability of 100% for both species. Irrespective of the temperature treatment, seeds of *A. nudicaulis* did not germinate in darkness, but achieved a high germinability from 15 to 40°C under red light (Tab. 1). A few seeds of *S. floribundus* germinated in darkness at 40°C, but under red light a high germinability was

Table 1: Temperature dependence of the germinability, average germination rate and average germination time of seeds of *Aechmea nudicaulis* (n=200 seeds/treatment). a) The treatments were conducted under red light, except indicated in the table. b) Germinability (G) of pooled isothermal replicates (in percent); Gi and Gs are the lower and the upper confidence limits of the germinabilities, respectively ($\alpha = 0.05$, Documenta Geigy, 1965). c) Calculated according to Labouriau (1972) (in hours). d) The seeds were incubated at 20/30° C (16/8 h, respectively) under continuous red light (Light) and in darkness. Because no seed germinated in darkness, they were exposed to red light treatment after 240 hours of incubation (Dark / light). e) Kolmogorov-Smirnov test for the normality of the germination curves. * Differs from a normal distribution; (Sokal & Rohlf, 1995). Statistica software 5.1.

Temperature ^a (°C)	Germinability ^b			Germination rate ^c (h ⁻¹ .10 ⁻⁴)	Rate variance ^c (h ⁻² .10 ⁻⁷)	Germination time ^c (h)	Time variance ^c (h ²)	Kolmogorov-Smirnov test ^e		
	Gi	G	Gs					Dmax	Lilliefors probability	
15	84.9	90	93.9	34.3	6.1	291.6	4392.24	0.250	0.003	*
20	98.2	100	-	97.9	25	102.12	272.07	0.338	0.015	*
25	98.2	100	-	100.8	69.7	99.24	67.6	0.369	0.025	*
30	98.2	100	-	98.4	21.7	101.64	231.43	0.418	0.002	*
35	90.9	95	97.6	54.4	42.3	183.75	4830.57	0.247	0.010	*
40	98.2	100	-	47.2	48.9	211.82	9840.69	0.345	0.000	*
45	38.0	45	52.2	28	21.7	356.76	35125.41	0.214	0.002	*
20/30 ^d										
Light ^d	87.9	92.5	95.7	70.2	19.6	142.44	805.22			
Dark / light ^d	95.7	98	99.0	133.4	19.7	74.94	62.21			

observed from 15 to 30°C (Tab. 2).

For both species the temporal distribution of the germination differed from a gaussian distribution in most incubation temperatures (Kolmogorov-Smirnov test, Tab. 1 and 2). The large variances of the average germination times at 15°C and above 35°C indicate for both bromeliads that the germination can prolong for a week or more at extreme temperatures (Tab. 1 and 2). The Mann-Whitney U-test pointed out the interval from 20 to 30°C as the optimum temperature range for germination of *A. nudicaulis*, and 25°C as the optimum temperature for germination of *S. floribundus* (Tab. 3).

Despite the low germinability at 45°C (Tab. 2), seeds of *S. floribundus* were still viable after 720 hours of incubation under red light and after 360 hours in darkness (tetrazolium test). When incubated at alternating temperatures of 20/30°C seeds of both species showed a high germinability only under red light (Tab. 1 and 2). The seeds in darkness were

transferred to red light after 240 hours of incubation and a high germinability resulted for both species (Tab. 1 and 2; Fig. 2). For both species no germination was detected at 20/50°C and the seeds were not viable after 720 hours of incubation (tetrazolium test pointed out zero percent of viability).

Temperature measurements at the study site showed that the minimum average temperature at the soil surface under plant cover ($21.5^{\circ}\text{C} \pm 0.8$) was similar to that observed in sunny areas ($21.0^{\circ}\text{C} \pm 0.9$). On the other hand, the maximum average temperature verified in soil exposed to full sunlight ($45.9^{\circ}\text{C} \pm 1.2$) was higher than that found in the shaded microhabitats ($28.3^{\circ}\text{C} \pm 4.5$).

Discussion

The occurrence of patches of plants interspersed by open areas results in different microclimates in the Restinga. Dau (1960) found that the daily thermal range in sheltered

Table 2. Temperature dependence of the germinability, average germination rate and average germination time of seeds of *Streptocalyx floribundus* (n=200 seeds/treatment). a) The treatments were conducted under light, except indicated in the table. b) Germinability (G) of pooled isothermal replicates (in percent); Gi and Gs are the lower and the upper confidence limits of the germinabilities, respectively ($\alpha = 0.05$, Documenta Geigy, 1965). c) Calculated according to Labouriau (1972) (in hours). d) The seeds were incubated at 20/30°C (16/8 h, respectively) under continuous red light (Light) and in darkness. Because no seed germinated in darkness, they were exposed to red light treatment after 240 hours of incubation (Dark / light). e) Kolmogorov-Smirnov test for the normality of the germination curves. * Differs from a normal distribution; NS, normal distribution (Sokal & Rohlf, 1995). Statistica software 5.1.

Temperature ^a (°C)	Germinability ^b			Germination rate ^c (h ⁻¹ .10 ⁻⁴)	Rate variance ^c (h ⁻² .10 ⁻⁷)	Germination time ^c (h)	Time variance ^c (h ²)	Kolmogorov-Smirnov test ^e	
	Gi	G (%)	Gs					Dmax	Lilliefors probability
15	87.5	92.5	98.3	33.2	2.9	300.84	2379.2	0.284	0.000 *
20	98.2	100	-	71.3	19.6	140.16	755.11	0.397	0.000 *
25	98.2	100	-	79.5	24	125.73	600.59	0.259	0.125 NS
30	98.2	100	-	60	16.5	166.55	1272.08	0.312	0.002 *
35	59.4	66.5	72.6	35.8	40.8	278.98	24738.34	0.229	0.000 *
40	16.9	22.5	28.4	32.1	25.3	311.47	23812.07	0.341	0.000 *
45	16.5	22	28.4	27.4	17.1	364.91	30396.18	0.348	0.000 *
40 - dark 20/30 ^d	16.9	22.5	28.4	27.9	27.8	358.93	46157.38		
Light ^d	96.0	98.5	99.5	60.9	8.03	163.98	580.33		
Dark / light ^d	85.0	89.5	94.0	93.7	29.5	106.73	382.64		

Table 3. Multiple binary comparisons of isothermal average germination rates (V) for four samples of 50 seeds of *Aechmea nudicaulis* and *Streptocalyx floribundus*, using a two-tailed Mann-Whitney test (Sokal & Rohlf 1995). The symbol * corresponds to U-values larger than the critical value $U_{0.05(4,4)} = 13$; lower U-values (non-significant differences at 0.05) are written in the nomogram.

<i>Aechmea nudicaulis</i>							<i>Streptocalyx floribundus</i>						
Temperature (° C)	15	20	25	30	35	40	Temperature (° C)	15	20	25	30	35	40
15							15						
20	*						20	*					
25	*	13					25	*	*				
30	*	7.5	12				30	*	*	*			
35	*	*	*	*			35	6	*	*	*		
40	*	*	*	*	*		40	10	*	*	*	11	
45	*	*	*	*	*	*	45	*	*	*	*	*	12

microsites is narrower than in sun-exposed microsites. Similar results were found by Franco *et al.* (1984) in a restinga located at Barra de Maricá (Rio de Janeiro State). While the minimum average temperature in the soil was similar in sites of different canopy densities (around 25°C), the maximum average temperature could reach 50°C or more in soil exposed to full sunlight (Franco *et al.* 1984). As

expected, we found that the maximum soil temperatures were higher in sunny than in shaded microhabitats.

An increase in incubation temperatures reduced the germinability for both species. At 35°C and above the germinability of *A. nudicaulis* was significantly higher than *S. floribundus*, but seeds of *S. floribundus* incubated at 45°C remained viable for more than

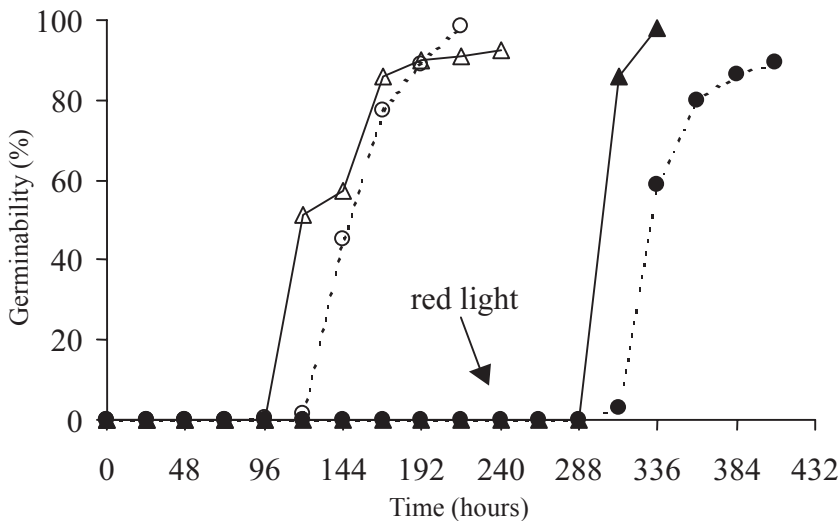


Figure 2. Germinability of seeds of *Aechmea nudicaulis* and *Streptocalyx floribundus* at 20/30° C. The seeds were incubated under red light (open symbols) and in darkness (black symbols) (n=200 seeds/treatment). After 240 hours of incubation in darkness the non-germinated seeds were exposed to red light. Continuous line - *A. nudicaulis*; Dashed line - *S. floribundus*.

30 days in light and 15 days in darkness. Although seeds of both species did not survive at alternating temperature of 20/50°C, the results suggest that at high temperatures *A. nudicaulis* is more likely to recruit from seeds than *S. floribundus*. Under permissive temperature regimes imbibed seeds of both species can remain viable for more than 10 days in absence of light, suggesting a capacity to constitute a transient soil seed bank in the restinga.

Seeds of *A. nudicaulis* germinated faster than seeds of *S. floribundus* in all temperatures tested, but even at the optimum temperature for germination (around 25°C) both species required at least four days in an imbibed state to germinate. Also, the time variances indicate for these bromeliads that germination extends for more than a week at temperatures of 35°C and above this. This suggests that under natural conditions a regular water availability is required for a successful germination, what restricts the seed recruitment for both species to sites where soil desiccation is not a recurrent phenomenon, as those occurring under plant cover (Franco & Nobel 1988; 1989; Fulbright *et al.* 1995; Barnes & Archer 1996).

In contrast to bromeliads of shaded habitats as gallery and deciduous forests (Garcia-Franco & Rico-Gray 1991; Rosa & Ferreira 1998), but similar to bromeliads of restinga as *Aechmea distichantha* and *Neoregelia cruenta* (Mercier & Guerreiro Filho 1990), seeds of *A. nudicaulis* and *S. floribundus* require light in order to germinate. Bromeliads that produce light-requiring seeds (Mercier & Guerreiro Filho 1990) were found to be shade-intolerant, as the case of *N. cruenta* and *A. nudicaulis* (Fischer & Araújo 1995). This suggests that the predominance of individuals of *A. nudicaulis* on the edges of the thickets could result from the shade-intolerance of the species.

The light and temperature requirements showed by seeds of *A. nudicaulis* and *S. floribundus* suggest that germination would

be limited to specific microsites where proper temperatures and light intensity were found. The seed susceptibility to high temperatures make these species unlikely to recruit from seeds in soils exposed to full sunlight. However, the seeds would find suitable conditions for germination in sheltered microhabitats. In fact, it has been proposed that the shade produced by the palm *Allagoptera arenaria* in the bare sand facilitate the germination of cacti and bromeliads as *A. nudicaulis* and *Neoregelia cruenta* (Scarano 2000). Subsequently, these species would favor the entry of woody species (as *Clusia* spp.), in a facilitation process resulting in the development of the thicket (Zaluar & Scarano 2000).

The results showed here suggest that the bromeliads *A. nudicaulis* and *S. floribundus* would not act as pioneers in patch dynamics but could participate as important intermediates in thicket formation by generating soil and microclimate conditions for the establishment of less tolerant species, as already addressed for *N. cruenta* (Hay & Lacerda 1980). Indeed, studies regarding plant growing in the field are necessary for a better understanding of the participation of these species in patch dynamics and to verify whether the bromeliads frequently found in the bare soil result from seed germination or clonal growth.

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