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Germination and vigor of long-pepper seeds (*Piper hispidinervum*) as a function of temperature and light[1]

Germinação e vigor de sementes de pimenta-longa (*Piper hispidinervum*) em função da temperatura e da luz

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ABSTRACT - The long pepper is considered a promising species because of offering the prospect of making Brazil self-sufficient in the production of safrole, an important essential oil used as a fixative for fragrances and having therapeutic properties. In establishing areas intended for the cultivation of this species, it is necessary to evaluate the physiological quality of the seeds used in the production of seedlings. The objective was to determine the conditions of temperature and luminosity for the test of germination and vigor in seeds of the long-pepper. Seeds from four different lots were used to make the following measurements: moisture content (105 ± 3 °C for 24 hours), germination (20; 25; 30 and 35 °C with photoperiods of 12 and 24 hours, and alternating between 20-30 °C and 20-35 °C with 12 hours of light at the higher temperature), speed of germination index, speed of germination, seedling dry matter, seedling emergence, emergence rate index and relative frequency of germination. The experimental design was completely randomized with averages being compared by the Tukey test ($P \leq 0.05$). The germination of long-pepper seeds can be assessed at 25 °C with 12h darkness - 12 h light, 25 °C with 24 h darkness, 30 °C with 12 h darkness - 12 h light and 30 °C with 24 h light, and the physiological potential at 30 °C with 24 h light.

Key words: Long pepper. Physiological potential. Forest seed.

RESUMO - A pimenta longa é considerada uma espécie promissora por apresentar a perspectiva de tornar o Brasil autosuficiente na produção de safrol, importante óleo essencial usado como fixador de fragrâncias e com propriedades terapêuticas. Na implantação de áreas destinadas à cultura dessa espécie é necessário avaliar a qualidade fisiológica das sementes utilizadas na formação de mudas. O objetivo foi determinar as condições de temperatura e luminosidade para o teste de germinação e vigor em sementes de pimenta longa. Foram utilizadas sementes de quatro lotes para as seguintes determinações: teor de água (105 ± 3 °C por 24 horas), germinação (20; 25; 30 e 35 °C com fotoperíodo de 12 e 24 horas, e alternadas de 20-30 °C e 20-35 °C, com 12 horas de luz na temperatura mais alta), índice de velocidade de germinação, velocidade de germinação, matéria seca de plântulas, emergência de plântulas, índice de velocidade de emergência e freqüência relativa da germinação. O delineamento experimental foi o inteiramente casualizado e as médias comparadas por Tukey ($P \leq 0,05$). A germinação de sementes de pimenta longa pode ser avaliada a 25 °C/12 h escuro - 12 h luz, 25 °C/24 h luz, 30 °C/12 h escuro - 12 h luz e 30 °C/24 h luz, e o potencial fisiológico a 30 °C/24 h luz.

Palavras-chave: Pimenta longa. Potencial fisiológico. Sementes florestais.

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INTRODUCTION

The Long Pepper (*Piper hispidinervum*), a shrub-like species of the Amazon region, has considerable commercial value in the production of safrole, an important secondary metabolite in obtaining heliotropine which is used as a fragrance, and piperonyl butoxide, used in the production of biodegradable insecticides (PEREIRA *et al*., 2008).

During germination, a sequence of physiological events occur that are influenced by temperature and light, making it necessary therefore, to study the influence of these factors in order to understand the germination process of seeds from species of different ecological groups (FERREIRA; FIGLIOLIA; ROBERTO, 2007), especially aromatic and forest species, for which basic information about the germination eco-physiology is still lacking.

The seeds of many of these species require specific temperature regimes in order to germinate due to the influence of the ecological characteristics of their habitat (SOUZA *et al*., 2007). For most tropical species, the optimum temperature for germination is between 15 and 30 °C (MACHADO *et al*., 2002). There are also species where germination is favored by an alternating daily temperature, but this need may be associated with dormancy, although an alternating temperature can accelerate the germination of non-dormant seeds (OAK; NAKAGAWA, 2000). Marcos Filho (2005) adds that the temperature needed for germination does not have a specific value, but may be expressed in terms of cardinal temperatures, i.e., minimum, maximum and optimum, the latter being defined as that at which maximum germination occurs in a relatively short time.

Light is not always a limiting factor in seed germination, but its presence can help to reduce problems caused by low water-potential in the soil, and the effect of temperatures higher than the optimum (MARCOS FILHO, 2005).

The effects of temperature and light on the germination of forest species has been studied as a way to assess which ecological conditions are more conducive to triggering the germination process in a natural environment (GODOI; TAKAKI, 2005). Besides providing information on the dynamics of germination in these environments, the definition of the optimum temperature and light conditions will assist in defining a protocol to evaluate germination (BRANCALION *et al*., 2008).

For the seeds of several forest and aromatic species detailed information exists about undertaking the germination test following the Rules for Seed Analysis - RSA (BRAZIL, 2009), but the Long Pepper is not even included in this publication, with there being little research work on the ideal conditions for germination and the physiological quality (ALMEIDA, 1999; BERGO *et al*., 2010), both basic parameters in a program of seed production.

The objective of this study was to determine the conditions of temperature and luminosity for the evaluation of the germination and physiological quality of the seeds of the Long Pepper.

MATERIAL AND METHODS

The work was carried out at the Laboratory of Seeds and Native Seedlings at the Foundation for Technology in Acre, and the Laboratory of Molecular Biology and Morphogenesis of Embrapa Acre, in Rio Branco, Acre, in 2009. Three batches of seeds of the Long Pepper were used, supplied by different local producers, and one lot belonging to the germplasm bank of Embrapa Acre. Spikelets were harvested when mature, ie, those which showed a black colouration, indicating physiological maturity. Soon after harvesting they were immersed in water for 24 hours, macerated in a polyethylene sieve of 230 mesh, washed in water to remove the mucilage, left to dry on sheets of newsprint for 72 hours in a ventilated place (PIMENTEL *et al*., 1998) and then subjected to the following evaluations: **moisture content**: determined by the greenhouse method (105 ± 3 °C for 24 hours) with two sub-samples of 0.31gm of seeds. The results were expressed as percentages (BRAZIL, 2009); **germination test**: four sub-samples of 50 seeds from each batch were placed in transparent acrylic boxes (11.0 x 11.0 x 3.5 cm) on two sheets of filter-paper moistened with de-ionized water at the ratio of three times the mass of the non-hydrated paper. The germination paper and de-ionized water were sterilised in a vertical autoclave (121 °C and 1 atm for 30 minutes). The boxes were placed in a BOD-type germinator at constant temperatures of 20; 25; 30 and 35 °C with 24 hours of light, 20; 25; 30 and 35 °C with light for 12 hours, and alternating temperatures of 20-30 °C and 20-35 °C with 12 hours of darkness at the lower temperature and 12 hours of light at the higher. For 30 days, the normal seedlings were computed daily, i.e. those where the root and shoot had fully developed; **germination speed index**: determined by a formula adapted from Maguire (1962) of the expression $IVG = (G_1/N_1) + (G_2/N_2) + ... + (Gn / Nn)$, where G_1 is equal to the number of seeds which had germinated at the first count, N1 is equal to the number of days elapsed for the first count, G_2 equals the number of seeds germinated at the second count, N_2 equals the number of days elapsed for the second count, and n, the final count; **germination rate**: determined by the number of days required for germination of 50% of the sample population (BEWLEY, BLACK, 1994); **seedling emergence**: sowing was carried out on polypropylene (Styrofoam ®) trays, each of 200 cells, holding sand which had been treated in an oven (120 ºC for 30 minutes), with four replications of 50 seeds from each batch. The trays were kept in the shade and received supplemental water daily. Assessments were made for 30 days, and those seedlings with hypocotyls of 5 mm at the time of evaluation were considered as emerged. The results were expressed as a percentage of the emerged seedlings; **emergence speed index**: determined through a formula adapted from Maguire (1962) by the expression = IVE (E_1/N_1) + (E_2/N_2) + ... + (En/Nn), where E_1 is equal to the number of seedlings at the first count, N_1 is equal to the number of days elapsed to the first count, G_2 equals the number of seedlings at the second count, N_2 equals the number of days elapsed to the second count, and n equals the last count; **seedling dry matter**: 30 seedlings of each subsample were wrapped in kraft paper and placed in an oven with forced air circulation, at 70 °C until reaching constant mass, determined with precision analytical scales (0.0001 g). The results were expressed in grams; relative frequency of germination: determined as a function of incubation time in the germinator, by the formula Fr = 100 ($ni /\sum ni$), where ni is the number of germinated seeds per day; $\sum ni$ is the sum of the total number of germinated seeds (LABOURIAU, 1983).

The experimental design adopted was completely randomized. The batches were analyzed separately for each combination of temperature and brightness, and the results submitted to variance analysis by the F test (5%). The Tukey test ($P \leq 0.05$) compared the averages when treatments were significant.

RESULTS AND DISCUSSION

The moisture content of the seeds of *P. hispidinervum* showed values of 17.4; 17.2; 17.3 and 18.4% for batches 1; 2; 3 and 4 respectively. With the combinations of 35 ºC/12 h light, 35 ºC/24 h light and alternating temperatures of 25 ºC/12 h dark-35 ºC/12 h light, germination was zero and therefore the data have not been presented, as too with the germination speed index, germination rate, seedling dry weight and relative frequency of germination. This result disagrees with that of Machado *et al*. (2002) who consider the maximum to be between 35 and 40 °C, i.e. seeds of tropical species should be tolerant to high temperatures. In this sense, there is an understanding that the presence of light can contribute to mitigating the effects of temperatures above the optimum for germination (MARK SON, 2005), but this was not observed at 35 ºC neither in 12 nor 24 hours of light.

High temperatures, albeit to a limited extent, are considered as optimal for the total germination of any one particular species, as they accelerate the biochemical processes involved in respiration, causing denaturation of the proteins and changes in membrane permeability, which lead to the loss of cellular material, a reduction in the supply of free amino acids, in the synthesis of proteins and in anabolic reactions (CARVALHO; NAKAGAWA, 2000). Marcos Filho (2005) adds that the effect of temperature is explained by enzymatic changes, by the physiological state of the seed or by the insolubility of oxygen under these conditions which increases demands and accelerates the respiratory activity of the seeds.

Seed germination from all batches was higher at 25 and 30 ºC compared to 35 ºC, which was zero (Table 1). This temperature variation is called thermo-inhibition and is characterized by the absence of germination when the temperature is slightly above the optimum. It is further noted that a constant temperature of 20 °C, especially in the presence of light for 24 hours, also limited the germination process of the seeds, but not so dramatically.

The treatment of 20 ºC/24 h was unique in that all batches showed inferior performance compared to the other treatments. Although light is cited as an environmental factor that can mitigate the consequences of suboptimal temperatures, its effects apply only to temperatures above the optimum (MARCOS FILHO, 2005), but when lower, the same benefits do not seem to be repeated.

The temperatures of both 25 and 30 °C in the presence of partial or total light, favoured a higher determination of the germination potential, with values between 67 and 98%, whereas for batches 1; 2 and 3, germination ranged from 89 to 98% at this temperature range, close to the average value of 91% found by Bergo *et al*. (2010) in seeds of the Long Pepper. This ability to germinate under different environmental conditions can have useful consequences, since for some seeds germination will occur irrespective of the conditions of their environment. These variations in the temperatures required by the species are an adaptive characteristic that give them a high capacity for establishing themselves in the field, since they allow the seeds to germinate at a higher range of temperatures. Batches 1 and 2 still managed to perform satisfactorily in the combinations of 20 ºC/12 h dark-12 h light, and 20 ºC/12 h dark and 30 ºC/12 h light. Accordingly, Carvalho and Nakagawa (2000) explain that more vigororous seeds germinate at a higher range of temperatures.

The germination speed index varied from 0.4 to 7.5 in batches 4 (20 ºC/24 h light) and 1 (30 ºC/24 h light) respectively, but the best combination was between 5.2

Table 1 - Germination (G%) and germination speed index (GSI) of seed batches of *Piper hispidinervum* as a function of temperature and luminosity

Temperature (°C)/Luminosity	Batches							
	G%				GSI			
	1	2	3	4	1	2	3	4
20 °C/12 h dark - 12 h light	91 a	77 a	50 c	59 bc	3.7 d	3.1 c	1.7 d	2.4 d
20 °C/24 h light	55 b	19 b	28 d	21 d	1.9 e	0.5 d	0.9 e	0.4 e
25 °C/12 h dark - 12 h light	96 a	89 a	94 a	72 abc	5.9 c	5.1 b	5.4 b	3.3 c
25 °C/24 h light	92 a	92 a	93 a	74 ab	6.5 b	6.0 ab	6.1 b	4.4 b
30 °C/12 h dark - 12 h light	98 a	90 a	92 a	67 abc	7.0 ab	5.9 ab	6.0 b	4.1 b
30 °C/24 h light	93 a	89 a	94 a	75 a	7.5 a	6.5 a	7.2 a	5.2 a
20 °C/12 h dark 30 °C/12 h light	94 a	89 a	79 b	59 c	5.8 c	5.5 ab	4.3 c	3.3 c
CV (%)	3.80	8.71	6.81	10.74	4.92	10.96	7.36	8.61

Averages followed by different letters in any one column differ at a level of 5% by the Tukey Test

and 7.5. Work values from Bergo *et al*. (2010) ranged from 4.67 to 7.05. It can be seen that 20°C/24 h light caused the greatest delay in germination for all batches. On the other hand, the combination of 30 °C/24 h was the only one where all of the batches were able to display their vigour, a result which was also verified in the germination test, although batch 2 also outperformed the other treatments of 25 °C/24 h light, 30 °C/12 h dark-12 h light, and 20 °C/12 h dark- 30 °C/12 h light, as did batch 1 in the treatment of 30 °C/12 h dark-12 h light. This result demonstrates that light influences the germination rate, as highlighted by Vidal *et al*. (2007) for seeds of *Conyza bonariensis* and *Conyza canadensis*, but this effect occurs only at appropriate temperatures.

Assessing the influence of temperature and light on the germination process of seeds of *P. hispidinervum* at constant temperatures of 20 and 25 °C in white light and diffuse light, and alternating 20 °C/16 h dark-30 °C/8 h white light, Bergo *et al*. (2010) found no significant differences between the tested combinations on the total germination, but the speed of the process was higher at 25 °C in white light of 720 lux, compared to the 120 lux of the diffuse light, i.e. the white light has an illuminating capacity six times higher than the diffuse light, a result that led the authors to conclude that in this species light also reduces germination time. In the present work, the highest germination speed also occurred in that treatment where the availability of light was greater.

In assessing the time required for the germination of 50% of the seeds (T_{50}), the treatment of 30 °C/24 h light yielded better results for all batches (Table 2), as also occurred in the tests for germination and the germination speed index (Table 1). For the seedlings, the same treatment favoured higher dry matter accumulation, as well as that of 25 °C/24 h light (Table 2), i.e. both with greater light availability. Brancalion *et al*. (2008) found that for the seeds of *jangada brava*, although they may have issued a primary root in the dark, the incidence of light also favored the development of the seedlings.

For Ferreira *et al*. (2010), the importance of the germination time is in the ability to evaluate the speed of occupancy of a species in a community. Accordingly, studies show that natural populations of Long Pepper typically occur in warm environments, with a direct incidence of light (ALMEIDA, 1999). The process of succession corresponds to the recovery of areas that after deforestation, will have changes in their microclimate which will determine the establishment of different species, depending on the ecological group to which they belong. Therefore *P. hispidinervum* would belong to the ecological group anthropic pioneers, whose seeds in general present positive photoblastism and/or thermoblastism, and germinate preferentially in open areas and clearings.

The response of the seeds to light is one of the factors controlling the germination time and can most often be seen in species with small seeds, such as the family Piperaceae. In these seeds, light serves more as a signal than as a resource for germination. Only adequate water, oxygen and temperatures are prerequisites for the growth of the embryo (BEWLEY, BLACK, 1994).

Germination, controlled by temperature and light is important for seedling establishment in forest clearings, which consist of environments with a large input of radiant energy (VAZQUEZ-YANES *et al*. 1990). This availability

Table 2 - Rate of germination (T50 days) and seedling dry matter (SDM g) of seeds of *Piper hispidinervum* as a function of temperature and luminosity by the test of germination

Temperature (°C)/Luminosity	Batches							
	T50				SDM			
	1	2	3	4	1	2	3	4
20 °C/12 h dark - 12 h light	24.7 a	25.5 a	29.2 a	27.2 a	0.88 b	0.87 b	0.88 b	0.88 b
20 °C/24 h light	nd*	nd	nd	nd	nd	nd	nd	nd
25 °C/12 h dark - 12 h light	15.7 b	16.8 b	17.0 c	20.4 bc	0.87 b	0.87 b	0.88 b	0.89 b
25 °C/24 h light	13.6 c	14.7 c	14.4 d	16.8 d	1.26 a	1.27 a	1.28 a	1.27 a
30 °C/12 h dark - 12 h light	13.5 c	14.7 c	14.9 d	17.6 cd	0.88 b	0.86 b	0.80 b	0.87 b
30 °C/24 h light	11.6 d	12.7 d	12.5 e	14.5 d	1.25 a	1.25 a	1.25 a	1.27 a
20 °C/12 h dark 30 °C/12 h light	15.5 b	15.8 bc	19.2 b	21.4 b	0.65 c	0.65 c	0.61 c	0.63 c
CV (%)	3.17	3.44	3.03	7.60	1.84	1.94	7.38	1.40

Averages followed by different letters in any one column differ at a level of 5% by the Tukey Test; (* nd: not determined)

of solar radiation influences the temperature variation, air humidity and soil temperature (PEZZOPANE *et al*., 2002).

In the work of Lima *et al*. (2006) with seeds of the Ironwood, a temperature of 30 °C was shown to be equally suitable for the optimization of the germination process, favouring germination and reducing the average time for its occurrence, while 35 °C produced a delay in germination. Also at 30 °C, seeds of the Baboonwood (*Virola surinamensis* (Rol.) Warb.), submitted to 25; 30 and 35 °C, germinated more intensely and in less time (FILES; SILVA; MORAES, 2007). These results reinforce the idea that most tropical and subtropical species show maximum germination potential at temperatures of up to 30°C (MACHADO *et al*., 2002).

The average germination of the four batches was over 80% in the combinations of 25 °C/12 h dark-12 h light, 25 °C/24 h light, 30 °C/12 h dark-12 h light, 30 °C/24 h light and 20 °C/12 h dark-30 °C/12 h light, and over 65% for 20 °C/12 h dark-12 h light. In the works of Almeida (1999), the total germination of seeds of the Long Pepper under a constant temperature of 25 °C and alternating temperatures of 25 °C 22 h/35 °C 2 h, 25 °C 20 h/35 °C 4 h and 25 °C 18 h/35 °C 6 h reached an average of 41.5%, while the germination rate was significantly lower under that treatment where the seeds were exposed for a longer time to 35 °C (25 °C 18 h/35 °C 6 h), which indicates a greater sensitivity to temperatures above 30 °C, although P. hispidinervum is considered to have adapted to hot areas (NUNES, 2004).

In seeds of *Heliocarpus popayanensis*, the temperature of 35 °C was beneficial to the seeds up to a maximum period of six hours (BRANCALION *et al*., 2008) as was seen in the present work, in a similar way to that observed in forest clearings. The fact that germination occurs at different temperatures and luminosities of 24 and 12 hours, indicates that the seeds of this species are able to germinate even in small clearings, indicating adaptation to the natural thermal and luminous fluctuations of the environment.

The emergence of seedlings in the greenhouse (Table 3) was lower than that of germination (Table 1), the difference probably being due to the laboratory conditions, which usually overestimate results compared

Table 3 - Emergence of seedlings (ES%) and rate of emergence index (REI) for seeds of *Piper hispidinervum*

Test	Batches				CV (%)
	1	2	3	4	
ES	31 BC	56 A	34 B	14 C	27.6
REI	7.3 B	14.8 A	9.0 AB	3.0 B	35.8

Averages followed by different letters in any one column differ at a level of 5% by the Tukey Test to in the field (GUEDES *et al*., 2009). This is expected because environmental conditions which are inadequate for the seed-germination processes are often observed in the field, causing seedling emergence there to be less than that obtained in the germination test in the laboratory.

Since the goal of the germination test is to determine the maximum germination potential of a batch of seeds, this being possible only because it is considered that the test conditions are highly favorable to the germination process, the combinations of 25 ºC/12 h dark-12 h light, 25 ºC/24 h light, 30 ºC/12 h dark-12 h light and 30 ºC/24 h light are the most suitable for the germination test of long pepper seeds, especially the latter, by allowing the formation of larger seedlings in less time.

For seedling emergence batch 2 stood out, and for the speed of emergence index batches1 and 4 were superior, a superiority already seen in the germination test (Table 1) when, along with batch 1, they germinated satisfactorily in 20 ºC/12 h dark-30 ºC/12 h light. Despite having been conducted under ambient conditions and in the shade, the light available in the emergence test, although not measured, and for only about 12 hours a day, may have been favourable to the rate of emergence, since not only the amount of radiation influences the photoblastic seeds, but also the light quality, as it is natural light.

This difference in germination and vigour among the batches may be due to the different environmental and management conditions to which each batch had been submitted, since they come from different places and producers, and the region of origin of the seeds, and events pre- and post harvest can interact with the genotype and consequently influence the conditions required for germination. The performance of a genotype is a result of the joint actions of the genotype, the environment and the interaction between these factors, this interaction reflecting the differences in the sensitivity of genotypes to environmental variations, resulting in changes in their development (ROCHA; VELLO, 1999) that can manifest themselves at germination.

Relative frequency polygons for germination (Figure 1), which determine the proportion of seeds germinated daily throughout the period of the experiment, and were determined only for those treatments where germination took place, showed polymodal and heterogeneous distribution over the batches at a constant temperature of 25 ºC/12 h dark-12 hours of light, with the start of germination being on the 14 th day for batch 1 and the 20 th day for the remainder. At alternating temperatures of 20 ºC/12 h dark-30 ºC 12 h light, in which all batches germinated from the 12 th day onwards, the distribution followed the same pattern, but evenly. For the combination of 20 ºC/24 h light, germination of the batches followed a unimodal distribution and the greatest peak in germination frequency occurred, but there was a noticeable delay in relation to the other treatments, beginning on the 24 th day; a delay also seen for the GSI (Table 1). Greater homogeneity and a tendency to a unimodal distribution occurred in treatments of 25 ºC/12 h dark-12 h light, 25 ºC/24 h light, dark 30 ºC/12 h dark-12 h light and 30 ºC/24 h light, where germination started 13; 12; 12 and 10 days respectively after sowing.

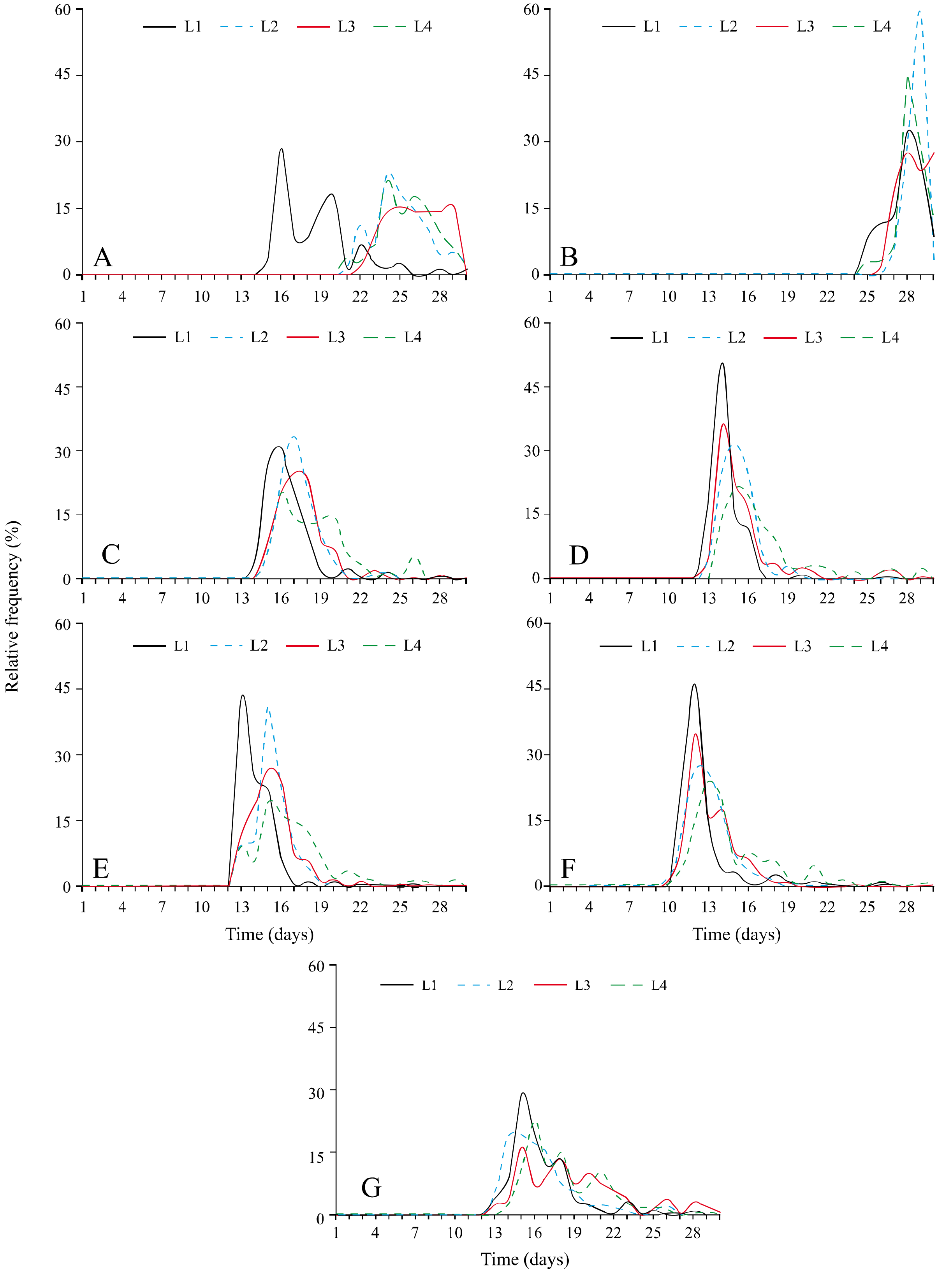
The better performance for germination of long pepper seeds at 25 ºC and especially at 30 ºC, may be related to the place of origin of the species, natural populations of which have so far only been found in the valley of the Acre river in Acre (EMBRAPA - BRAZILIAN COMPANY FOR AGRICULTURAL RESEARCH, 1998), which presents minimum, average and maximum temperatures of 16; 24.5 and 32 ºC respectively (MOSQUE, 1996). The most favorable temperature for germination usually varies within the range of temperatures found at the ideal location for seedling emergence and establishment (RAMOS; VARELA, 2003; SOUZA et al., 2007).

Therefore, 25 ºC and 30 ºC would appear to be the minimum and maximum temperatures respectively, the latter being the one where maximum germination occurred in a relatively short time, confirming Marcos Filho (2005).

As regards luminosity, the treatment of 30 ºC/24h light, which allowed greatest dry matter accumulation, increased the speed of germination and reduced the time required for 50% of the seeds to germinate, it was the treatment that provided light for longer and thus demonstrated the influence of this environmental factor on the rate of germination, as pointed out by Vidal *et al*. (2007).

These results, in addition to providing information on the dynamics of germination in natural environments (BRANCALION *et al*., 2008), allow further knowledge about the germination process of long pepper seeds, in such a way as to provide help in establishing a protocol to evaluate the germination and vigour of the species, taking into consideration that there are already studies with recommendations for the production of long pepper seedlings (PIMENTEL *et al*., 1998), whose seeds are sold by Embrapa in Acre; a unit that has conducted research for over a decade into implementing a sustainable system of production (NUNES, 2004).

Figure 1 - Effect of treatments on the distribution of the relative frequency of germination of the seeds of *Piper hispidinervum* during the period of incubation for the combinations of 20 °C/12 h dark-12 h light (A), 20 °C/24 h light (B), 25 °C/12 h dark-12 h light (C), 25 °C/24 h light (D), 30 °C/12 h dark-12 h light (E), 30 °C/24 h light (F) and 20 °C/12 h dark-30 °C/12 h light (G)



CONCLUSION

Germination of the seeds of the Long Pepper can be evaluated at 25 °C/12 h dark-12 h light, 25 °C/24 h light, 30 °C/12 h dark-12 h light and 30 °C/24 h light, and physiological potential at 30 °C/24 h light.

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