Germination requirements and seedling establishment of four dry forest species from Nicaragua

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Abstract: We examined the optimal temperature and light requirements for seed germination of *Bombacopsis quinata*, *Cordia alliodora*, *Lysiloma divaricatum* and *Tabebuia rosea* and establishment of *B. quinata*, *C. alliodora* and *T. rosea* seedlings planted under different light conditions. Seeds of *L. divaricatum* germinated rapidly and to a large extent at all constant temperature regimes (15-35 °C) both in light and darkness. Exposure of seeds to alternating temperatures of 20/15 °C resulted in 58 % germination in darkness and 62 % in light. *C. alliodora* and *T. rosea* seeds germinated equally well at constant temperature regimes ranging from 20 °C to 35 °C in light and darkness. Exposure to alternating temperatures (20/15 °C) resulted in higher germination for seeds of *C. alliodora* in dark than in light, while it inhibited the germination of *T. rosea* seeds. Seeds of *B. quinata* incubated at 20 °C and 25 °C in light and 20 °C in darkness exhibited the highest germination while exposure to alternating temperatures completely arrested germination in this species. Survival of *C. alliodora* seedlings was higher on open and partially-open sites than on the site under closed canopy. *B. quinata* had the lowest survival while *T. rosea* had the highest on the open site. The findings are discussed in relation to the restoration of abandoned sites. We concluded that while *C. alliodora* and *T. rosea* could potentially serve as framework species for the restoration of degraded and/or abandoned sites, *B. quinata* does not meet the requirements of a framework species for restoring degraded sites in drier regions.

Resumen: Examinamos la temperatura óptima y los requerimientos lumínicos para la germinación de semillas de *Bombacopsis quinata, Cordia alliodora, Lysiloma divaricatum* y *Tabebuia rosea*, y el establecimiento de plántulas de *B. quinata*, *C. alliodora* y *T. rosea* plantadas en diferentes condiciones de luz. Las semillas de *L. divaricatum* germinaron rápidamente y en gran medida en todos los regímenes de temperatura constante (15-35 °C) tanto en la luz como en la oscuridad. La exposición de las semillas a temperaturas alternantes de 20/15 °C resultó en una germinación de 58 % en la oscuridad y de 62 % en la luz. Las semillas de *C. alliodora* y *T. rosea* germinaron igualmente bien en regímenes de temperatura constante de entre 20 °C y 35 °C, tanto en la luz como en la oscuridad. La exposición a temperaturas alternantes (20/15 °C) provocó una germinación de las semillas de *C. alliodora* más alta en la oscuridad que en la luz e inhibió la germinación de las semillas de *T. rosea*. Las semillas de *B. quinata* incubadas a 20 °C y 25 °C en la luz y 20 °C en la oscuridad mostraron la germinación más alta, mientras que la exposición a temperaturas alternantes detuvo completamente la germinación en esta especie. La supervivencia de plántulas de *C. alliodora* fue mayor en los sitios total y parcialmente abiertos que en el sitio con dosel cerrado. *B. quinata*

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tuvo la supervivencia más baja, mientras que *T. rosea* tuvo la más alta en el sitio abierto. Se discuten los hallazgos en relación con la restauración de sitios abandonados. Concluimos que mientras *C. alliodora* y *T. rosea* podrían servir potencialmente como especies de referencia para la restauración de sitios degradados o abandonados, *B. quinata* no cumple con los requisitos para ser una especie de referencia para restaurar sitios degradados en regiones más secas.

Resumo: No presente trabalho examinou-se a temperatura ideal e as necessidades de luzpara a germinação de sementes de *Bombacopsis quinata, Cordia alliodora, Lysiloma divaricatume Tabebuia rosea* e o estabelecimento de mudas de *B. quinata, C. alliodorae T. rosea* plantadas sob diferentes condições de luz. As sementes de *L. divaricatum* germinaram rapidamente e, em larga medida, em todos os regimes de temperatura constante (15-35 °C),quer em ambiente iluminado quer no escuro. Aexposição das sementes a temperaturas alternadas de 20/15 °C resultou em 58 % de germinação no escuro e 62 % na luz. As sementes *C. alliodora* e de *T. rosea* germinaram igualmente bem em regimes de temperatura constante entre 20 °C a 35 °C na luz e na escuridão. A exposição à alternância de temperaturas (20/15 °C) resultou numa maior taxa de germinação de sementes de *C. alliodorae* que foi mais acentuada no escuro do que sob luz, enquanto inibiu a germinação das sementes de *T. rosea*. Já as sementes de *B. quinata*, incubadas a 20 °C e 25 °C sob luz e a 20 °C no escuro, apresentaram a maior germinação, enquanto a exposição a temperaturas alternadas a inibiram completamente. A sobrevivência das plântulas de *C. alliodorafoi* maior em locais abertos ou parcialmente abertos do que em locais sob dossel fechado. A B. quinataapresentou a menor sobrevivência, enquanto a *T. roseaa presentou* a taxa mais elevada no site aberto. Os resultados são discutidos em relação à restauração de estações abandonadas. Concluiu-se que embora a *C. alliodorae* a *T. roseasejam* espécies que podem servir de base para a recuperação de áreas degradadas e / ou locais abandonados, a *B. quinatanão* preenche os requisitos de uma espécies quadro para recuperação de áreas degradadas em regiões mais secas.

Introduction

The dry deciduous forests cover an area of 100 000 hectares in Nicaragua (Alves-Milho 1996). Historically, this forest formation has been extensively converted to other land use types, such as agriculture and/or pasture (Janzen 1988; Sabogal 1992). The last remnants of these forests occur as fragmented patches situated along the Pacific coast. Dry forests are considered to be the most degraded and endangered forests in the country (Sabogal 1992). In recent years, there is also an increasing tendency of abandonment of agricultural fields leading to the development of secondary forests (Castro-Marín *et al.* 2005). These degraded forests and abandoned agricultural fields urgently require measures to recover the original forest ecosystem; abandoning agricultural land has become a common event in the recent decades due to a shift in the economic interest (Castro-Marin *et al.* 2009a).

One effective strategy for forest restoration is the 'framework species' approach (Goosem & Tucker 1995; Lamb *et al.* 1997; Tucker & Murphy 1997). A 'framework species' is a species with high survival and growth rates in the open degraded sites, and which develops dense spreading crowns that rapidly shade out herbaceous plants and provide resources for wildlife at an early stage (Goosem & Tucker 1995). The method, basically, involves planting of 20 - 30 native tree species, both pioneer and climax, in a single step. Selecting candidate framework species, however, requires extensive background studies from germination trials to early seedling survival and growth. Blakesley *et al.* (2002) have examined the potential of 36 species as framework species in northern Thailand based on seed germination characteristics, and Elliot *et al.* (2003) evaluated field performance of these species after the second wet season.

Open sites often experience higher light intensity, lower surface soil moisture and fluctuation in diurnal temperature regime (Bullock 2000) compared to the forest understorey environment, depending on the canopy architecture. Temperature and light conditions play an important role in the germination of seeds and establishment of seedlings. Temperature is the most important environmental factor responsible for the synchronization of germination with conditions suitable for seedling establishment (Probert 2000). It regulates germination by determining the capacity and rate of germination, by removing primary and/or secondary dormancy, and by inducing secondary dormancy (Bewley & Black 1994). Thus, for any non-dormant seed population, germination occurs within well defined temperature limits, and three cardinal temperatures can be recognized over a short period, minimum, optimum and maximum, at which germination will occur. Earlier studies have demonstrated that seeds of many tropical forest trees germinate readily at constant temperatures of 20 - 30 °C, but the optimal germination temperature varies among species (Khurana & Singh 2001; Teketay 1996). Light intensity and its spectral quality (red : far red ratio) also influence the germination, survival and growth of seedlings of tropical tree species with marked inter-specific variation (Guariguata 2000; Khurana & Singh 2001; Ray & Brown 1995; Rincon & Huante 1993).

Compared to rain forest species, there is a lack of studies on seed germination, establishment and growth of seedlings of tropical dry forest species (Gerhardt 1993, 1996; Gerhardt & Hytterborn 1992; Teketay 1996). Seed germination and seedling establishment are demographically critical phases in the regeneration of plants from seeds (Khurana & Singh 2001; Kozlowski 2002; Teketay 1996), thus an understanding of factors influencing seed germination, survival and growth of seedlings of native species is vital for designing appropriate restoration technique. Such information is generally lacking for native tree species of Nicaragua. Thus, the present study was performed with the aim of examining the potential of four dry forest species, *Bombacopsis quinata* (Jacq.) Dugand., *Cordia alliodora* (Ruiz & Pavon) Oken, *Lysiloma divaricatum* (Jacq.) and *Tabebuia rosea* (Bertol.) DC. as framework species through their seed germination and seedling performance under different conditions. We investigated the seed germination of these four species in relation to different constant and alternating temperature regimes as well as light conditions. Survival and growth of transplanted

seedlings over one year period, in relation to the degree of canopy openness, was also studied. The species were selected based on their economic, social and ecological significances.

Materials and methods

Tree species

The species investigated in the present study were *B. quinata*, *C. alliodora*, *L. divaricatum* and *T. rosea*. *B. quinata* (Bombacaceae) is a large deciduous tree, widely distributed in deciduous and evergreen forests of Central America and north of South America. It is commonly found in areas receiving 800-2200 mm rainfall and experiencing temperatures from 20 to 27 °C. The number of seeds per kilogram is from 39,600 to 41,500. Standard laboratory germination test showed that fresh seed germination ranges from 70 to 80 %. The seeds are about 5 mm long and 3 mm wide (Cordero *et al.* 2004; Steven *et al.* 2001).

C. alliodora (Boraginaceae) is widely distributed in deciduous and evergreen forests of Central (Mexico) and South America (South of Brazil and North of Argentina). It is an early colonizer, and medium to large-sized deciduous tree, occur in an area receiving 1000-4000 mm annual rainfall and experiencing temperatures between 18 and 32 °C. The number of seeds per kilogram is around 105,000 and seeds are often dispersed by wind. On average, the seed is 8 mm long and 1 mm wide (Cordero *et al.* 2004; Steven *et al.* 2001).

L. divaricatum (Fabaceae) is a small to medium-sized legume tree, widely distributed in deciduous and evergreen forests of Mexico and Central America. This species occurs where the mean annual rainfall ranges from 800 to 1800 mm and mean annual temperature ranges from 24 - 30 °C. There are around 31,500 - 35,000 seeds per kilogram. The germination percentage of fresh seeds varies from 70 to 80 %. Seeds are about 7 mm long and 4 mm wide (Cordero *et al.* 2004; Steven *et al.* 2001).

T. rosea (Bignoniaceae) is a deciduous and medium to large-sized tree, widely distributed in deciduous and evergreen forests of Mexico, Brazil, Colombia, Ecuador, Peru and Venezuela. It occurs in areas receiving 1500 - 2500 mm annual rainfall and with mean annual temperature higher than 26 °C. There are around 44,100 - 55,000 seeds per kilogram. The germination of fresh seeds varies between 70 and 95 %. An average seed is 13 mm long and 6 mm wide (Cordero *et al.* 2004; Steven *et al.* 2001).

Seed material

Seeds were purchased from a company "Semillas Forestales del Tropico S. A." in Nicaragua. *B. quinata, C. alliodora* and *T. rosea* seeds were collected from San Francisco, San Marcos, Carazo, La Curva Belen, Rivas and La Isla de Ometepe, Rivas, Nicaragua, respectively. *L. divaricatum* seeds were collected from La Cuesta, Teustepe, Boaco, Nicaragua. Seeds were packed in plastic bags and transported to the Swedish University of Agricultural Sciences, Department of Silviculture, Forest Seed Science Centre, Umeå, where the experiment was conducted. They were stored for about three weeks at 5 °C until the study was carried out.

Seed germination experiment

A 2 × 7 factorial experiment was set-up to investigate the effects of light and temperature on seed germination of the selected species. The temperature regime had seven levels: five constant temperature regimes (15, 20, 25, 30 and 35 °C) and two alternating temperatures, 20/15 °C and 25/15 °C each with a thermoperiod of 12 hours. The alternating temperatures were chosen in line with the prevailing natural conditions during the rainy season when most of the seeds start to disperse and germinate. Two levels of light condition, exposure to continuous light from fluorescent lamp F40 w/33 RS cool white light (light intensity = $20 \mu Em^{-2}s^{-1}$) and incubation in the dark, were used for examining the light requirement for germination.

The germination test was performed on plates with pits using standard germination paper (Munktell analytical filter paper, 75 mm diameter) as the germination substrate. Each germination plate had 12 pits and the size of each pit was 7 cm in diameter and 3 cm in depth. Each pit was filled with de-ionized water and covered with aluminum foil with a crevice in the middle. One piece of germination paper, also with a crevice, was placed on top of the aluminum foil. Two stripes of narrow germination paper were inserted through the crevices of the germination paper and the aluminum foil into the de-ionized water in the pit. Another piece of germination paper with 25 seeds per replication was placed on top. Each set of seeds was then covered with a bell jar (black jars for dark experiments and white transparent jars for light experiments) with a small hole at the side of the upper part to allow gas exchange. Such an arrangement enabled continuous uptake of water by seeds throughout the test period without disturbing the experiment; especially the dark experiment. Finally, the germination plates were placed in growth chambers at preset constant and alternating temperature regimes. For each species, a total of 100 seeds, four replicates of 25 seeds each, were used in each treatment. The germination test was run for 21 days for all species. The germination process was monitored every day for seeds incubated in continuous light and seeds were considered germinated when the radicle reached 2 mm and had normal appearance. For dark incubated seeds, the final germination count was made after 21 days.

Seedling establishment experiment

The seedling establishment experiment involved three species, *B. quinata, C. alliodora* and *T. rosea*, as seeds of *L. divaricatum* were scarce during the time of seedling production in the nursery. Seedlings were raised in the Ministry of Natural Resources and Environment nursery in Managua, Nicaragua. Six-month-old seedlings were transplanted under three different canopy covers, open, partially-open and under the relatively closed canopy of dry deciduous forest in Chacocente National Wildlife Refuge. Description of the planting site can be found elsewhere (Castro-Marín *et al.* 2005). The canopy cover was determined using the spherical densitometer as 0 % for open, 50 % for partially-open and 100 % for closed canopy. For each species, a total of 20 seedlings were transplanted at a spacing of 1 × 1 m. Each individual seedling was tagged, and the height and root collar diameter were measured. The initial mean root collar diameter at the time of planting was 2.2 ± 0.1, 4.3 ± 0.2 and 2.3 ± 0.2 mm for *B. quinata, C. alliodora* and *T. rosea*, respectively. The corresponding height was 18.8 ± 0.5, 24.7 ± 1.1 and 15.2 ± 0.5 cm. A second measurement was carried out in August 2004 to evaluate survival and growth of planted seedlings.

Data analyses

For germination experiment, the germination capacity (GC) and the mean germination time (MGT) were calculated for each treatment as follows:

$$GC(\%) = \left(\frac{\sum n_i}{N} \right) \times 100$$

$$MGT(days) = \left(\frac{\sum (t_i n_i)}{\sum n_i} \right)$$

where, N is the total number of seeds sown, t_i is

the number of days starting from the day of sowing and n_i is the number of seed germinated on each day (Bewley & Black 1994). The percentage germination data set was arcsine transformed before analysis (Zar 1996), and two-way ANOVA was performed to test for significant differences among temperature regimes and light conditions for each species separately. For statistical analysis, the mean germination time was considered for species and treatments that showed some germination in all the replicates and one-way ANOVA was used to detect the significant differences in MGT. Means that showed significant differences were compared using Tukey's test at the 5 % level of significance.

For the seedling establishment and growth experiment, survival, height and root collar diameter were assessed after one year of transplanting. A Chi-square analysis of 3×3 contingency table was performed to test the null hypothesis that seedling survival is independent of canopy cover. This was followed by a separate Chi-square goodness-of-fit test to examine whether survival of planted seedlings varied among species and canopy cover. The current annual increment (CAI) in root collar diameter was computed for *C. alliodora*, as survival of the other two species was extremely low. One-way unbalanced ANOVA was performed to examine the differences in CAI among canopy cover using each individual seedling as a replicate. CAI in height was not computed for any of the species, as the majority of individual seedlings were clipped by herbivores, resulting in negative growth rate.

Results

Seed germination

Seed germination of the selected species responded differently to temperature regimes and light conditions. The germination capacity of *B. quinata* seeds varied significantly with respect to light conditions ($F_{1,42} = 69.121$; $P < 0.001$), temperature regimes ($F_{6,42} = 157.369$; $P < 0.001$) and their interaction ($F_{6,42} = 11.480$; $P < 0.001$). Seeds of this species incubated at 20 and 25 °C under continuous light had the highest germination capacity, followed by 20 °C in darkness (Fig. 1). Seeds of *B. quinata* did not germinate at 15 °C and under alternating temperature regimes (20 °C/15 °C and 25 °C/15 °C) under both continuous light as well as darkness. The mean germination time of seeds of this species exposed to continuous light varied significantly ($F_{3,12}$

= 9.360; $P < 0.001$) among temperature regimes. The speed of germination, as determined by the mean germination time, of *B. quinata* seeds incubated at 20 and 25 °C was faster than the rest of temperature regimes examined (Fig. 2).
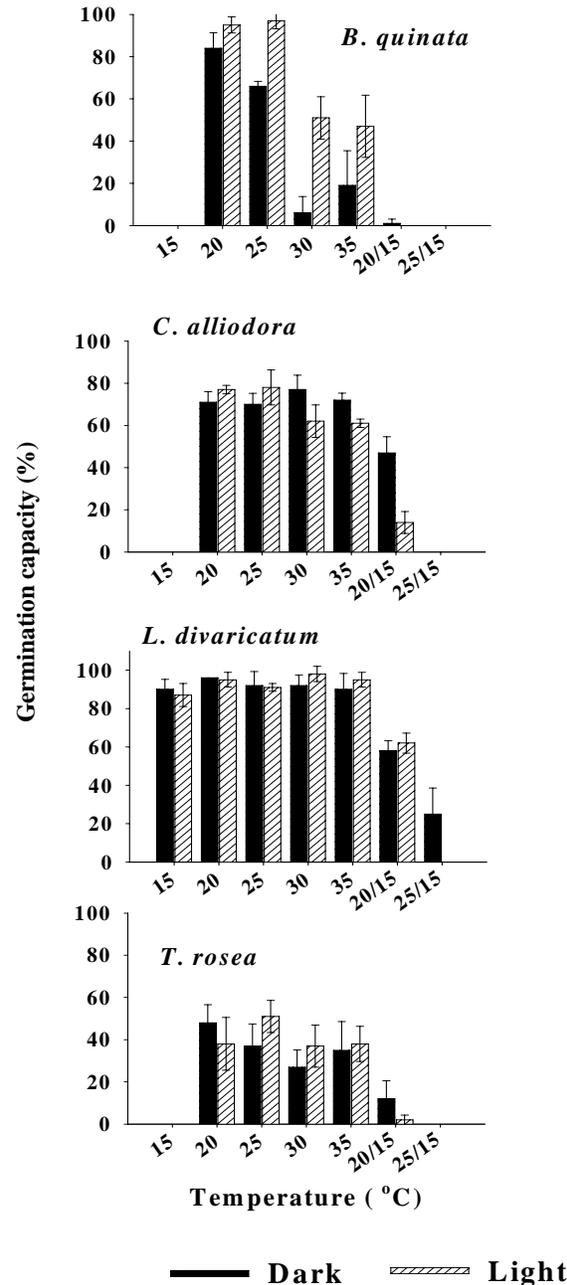

Fig. 1. Germination capacity (%) of seeds of *B. quinata, C. alliodora, L. divaricatum,* and *T. rosea* in response to different temperature regimes and light conditions (mean ± SE).

The germination capacity of *C. alliodora* seeds varied significantly in response to different temperature regimes ($F_{6,42}$ = 254.927; P < 0.001), as well as light conditions ($F_{1,42}$ = 15.426; P < 0.001) and for the interaction ($F_{6,42}$ = 13.000; P < 0.001). Irrespective of the light conditions, germination was inhibited when seeds were incubated at 15 °C and alternating temperature of 25/15 °C (Fig. 1). For seeds exposed to continuous light, germination capacity was significantly higher at 20 °C and 25 °C compared with 30 °C and 35 °C. In darkness, germination capacity was equally high for seeds incubated at 20 °C to 35 °C. The mean germination time varied significantly ($F_{4,15}$ = 9.298; P = 0.001) among the different temperature regimes under continuous light condition for *C. alliodora*. Seeds of this species incubated at 35 °C germinated faster than those exposed to other temperature regimes (Fig. 2).

Seeds of *L. divaricatum* germinated equally well under continuous light and darkness, and no significant difference in germination capacity between continuous light and darkness was found. However, temperature and its interaction with light conditions had a significant ($F_{6,42}$ = 65.554; P < 0.001 for temperature regimes; $F_{6,42}$ = 2.346; P = 0.048 for the interaction) effect on the germination capacity of *L. divaricatum* seeds. Under both continuous light and darkness, germination capacity was much higher when seeds were incubated at constant temperature than alternating temperature regimes (Fig. 1). While seeds incubated under continuous light at 25/15 °C did not germinate at all, dark-incubated seeds at the same alternating temperatures had a germination capacity of 25 %. The speed of germination showed a significant ($F_{5,18}$ = 200.588; P < 0.001) difference with respect to different temperature regimes under continuous light condition. Seeds of *L. divaricatum* incubated at 25 °C and 30 °C germinated rapidly compared with the rest of temperature regimes evaluated (Fig. 2).

For *T. rosea* seeds, germination capacity varied significantly among the different temperature regimes ($F_{6,42}$ = 45.347; P < 0.001), but not between light conditions. The interaction between light conditions and temperature regimes significantly affected ($F_{6,42}$ = 2.592; P = 0.032) the germination capacity of *T. rosea* seeds. Germination was completely inhibited at 15 °C and 25 °C/15 °C irrespective of the light conditions (Fig. 1). Seeds incubated at constant temperatures (20 - 35 °C) germinated fairly well both in light and darkness compared with those exposed to alternating temperatures. The mean germination time also varied significantly ($F_{3,12}$ = 8.976; P =

0.002) among the different temperature regimes. It was shorter for seeds incubated at 35 °C than either 20 °C or 30 °C (Fig. 2).
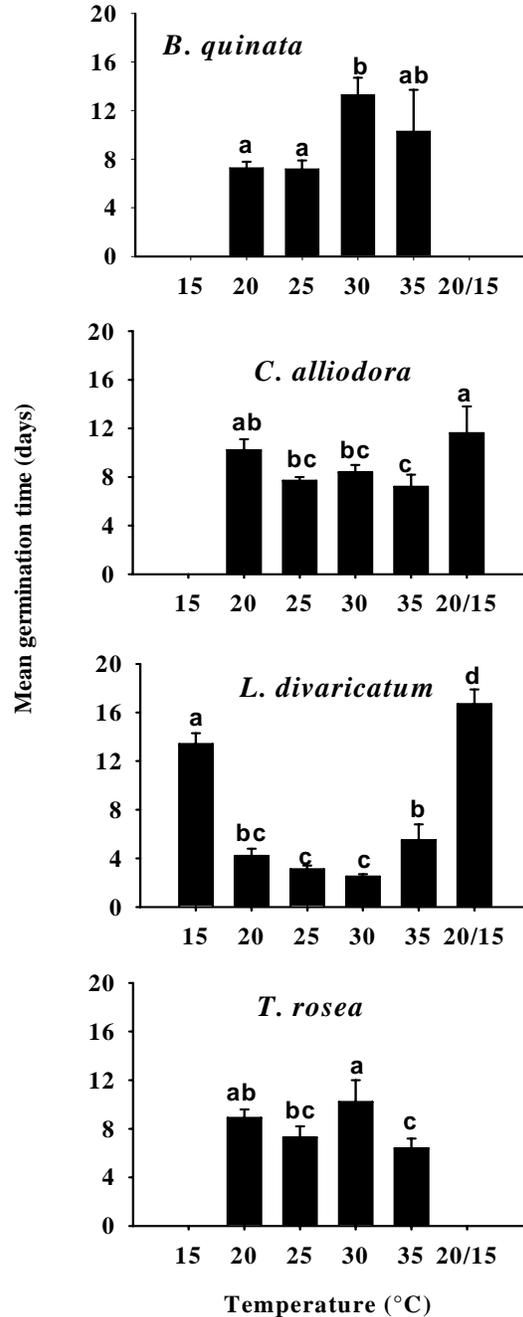

Fig. 2. Mean (± SE) germination time of four Nicaraguan tree species in response to different temperature regimes. Means with different letters are significantly different from each other at $P \leq$ 0.05.

Survival and growth of seedlings

A Chi-square analysis of 3×3 contingency table revealed that seedling survival of the selected species was strongly dependent on the degree of canopy cover ($\chi^2_{0.05, 4} = 14.457$; $P = 0.006$). For *B. quinata* seedlings, survival was relatively higher on open and partially-open sites compared with closed canopy where no seedling survived (Table 1). A similar trend was observed for *C. alliodora* seedlings, although survival for this species was relatively higher under closed canopy compared with *B. quinata* and *T. rosea* seedlings. *T. rosea* seedlings planted on partially-open site and under closed canopy did not survive at all. As a whole, survival of *C. alliodora* seedlings was significantly higher ($\chi^2_{0.05, 2} = 28.12$; $P < 0.001$) than the other two species at all levels of canopy cover. For all species combined, survival was significantly higher for seedlings planted on open site, followed by those planted on partially-open site ($\chi^2_{0.05, 2} = 12.16$; $P = 0.002$).

Table 1. Survival (%) of seedlings of three dry forest species planted under different canopy cover, after one year.

Canopy cover	*B. quinata*	*C. alliodora*	*T. rosea*	Total
Open	10	65	55	43
Partially-open	15	75	0	30
Closed canopy	0	30	0	10
Total	8	57	18	

Seedlings of *B. quinata* had extremely low survival in open and partially-open sites and did not survive at all under closed canopy while *T. rosea* seedlings did not survive at all on partially-open and closed canopy sites. Consequently, CAI in root collar diameter is reported for *C. alliodora* seedlings only. CAI in root collar diameter varied significantly ($F_{2,31} = 7.358$; $P = 0.002$) among differential canopy cover sites. *C. alliodora* seedlings planted on open site had higher increment in collar diameter compared with those planted on partially-open site or under closed canopy (Table 2). It was not possible to compute CAI in height due to severe clipping caused by herbivores.

Discussion

Seed germination

Temperature is the most important environ-
mental variable responsible for the synchronization of germination with conditions suitable for seedling establishment (Probert 2000). Thus, any non-dormant seed population germinates within well defined temperature limits, and three cardinal temperatures can be recognized over the short period: minimum, optimum and maximum. Seeds of *L. divaricatum* had higher germination across temperatures, 15 - 35 °C, both in continuous light and darkness. However, despite the high degree of thermo-plasticity, the speed of germination, a parameter often related to temperature, was significantly faster for seeds incubated at 25 - 30 °C. Therefore, the optimal temperature for seed germination of this species appears to be 25 - 30 °C, which is in conformity with the temperature conditions of its natural habitat (Cordero *et al.* 2004; Steven *et al.* 2001).

Table 2. Current annual increment (CAI) in root collar diameter of *C. alliodora* seedlings planted under different canopy cover together with diameters at the time of planting (D1) and after one year of growth (D2). Means followed by different letters across the column are significantly different from each other at $P \leq 0.05$.

Canopy cover	N*	D1 (mm)	D2 (mm)	CAI (mm)
Open	13	3.52 ± 0.37	7.95 ± 0.60	4.43 ± 0.73a
Partially-open	15	4.81 ± 0.43	6.82 ± 0.43	2.01 ± 0.28b
Closed canopy	6	5.33 ± 0.19	7.18 ± 0.65	1.85 ± 0.39b

* N = number of survived seedlings.

The germination of the other three species, *viz. B. quinata, C. alliodora* and *T. rosea* was completely arrested when the seeds were incubated at 15 °C both in continuous light and darkness. This is possibly related to induction of secondary dormancy, as seeds which remained ungerminated were still intact (pers. obs). A similar finding has been reported for *Moringa stenopetala* (Bak. f.) Cuf. where seeds initially placed at 10 °C and 15 °C did not germinate but as high as 58 % and 70 % germination were recorded when they were transferred to 20 °C and 25 °C, respectively (Teketay 1995). The optimal temperature for germination of *B. quinata* and *C. alliodora* seeds appeared to be 20 - 25 °C beyond which germination started to decline. This range is typical for many tropical tree species (e.g. Delachiave & De Pinho 2003; Teketay 1996; Teketay & Tigabu 1996; Teketay & Granström

1997; Tigabu & Odén 2001; Yirdaw & Leinonen 2002; Zida *et al*. 2005). For *T. rosea*, no apparent optimal temperature could be determined, as germination capacity and speed of germination did not show distinct differences among constant temperature regimes between 20 °C and 35 °C. This could be related to the inherent quality of the seed lot used in the present study. In a study made by Gómez & Rojas (2004), 92 % germination was found for *T. rosea* seeds incubated at 30 °C in a photoperiod of 12 h.

The alternating temperature regimes tested in the present study did not result in beneficial effect on germination compared with the constant temperature regimes. Sensitivity to alternating temperatures depends on amplitude (the difference between the maximum and minimum temperature), thermoperiod (time in hours each day above the mean temperature) and number of temperature cycles (Ekstam & Forseby 1999; Ekstam *et al*. 1999; Probert 2000). Our study showed that germination of *L. divaricatum* and *C. alliodora* seeds decreased with increasing amplitude while that of *B. quinata* and *T. rosea* seeds did not respond at all to alternating temperature. This suggests that sensitivity to alternating temperatures is species-specific, and each species has an optimum amplitude for germination. Teketay (2002) pointed out that higher amplitude may be associated with high evapotranspiration, thereby creating rapid desiccation of the germination substrate. It may be pointed out that *C. alliodora* and *T. rosea* seedlings performed well on partially-shaded and open sites, respectively. Such a response to alternating temperatures could result in patchy regeneration under natural conditions; leading to aggregated distributional pattern of seedling populations (Castro-Marin *et al*. 2009b).

The sensitivity of seed populations to alternating temperatures may be influenced by other environmental factors, particularly light. This is evident for *C. alliodora* where seeds incubated at alternating temperatures of 20/15 °C in darkness had a significantly higher germination (47 %) than seeds incubated at the same alternating temperatures in light (14 %). Thompson *et al*. (1977) reported that some species require light to germinate at constant temperature, but they can germinate in light and darkness at alternating temperatures. The interaction between the active form of phytochrome (P_{fr}) and a requirement for alternating temperatures is well recognized, and Probert & Smith (1986) suggested that the capacity for dark germination at alternating temperatures may be explained by the sensitivity of some individual seeds to low level of pre-existing P_{fr}.

Seeds of the present species exhibited different germination responses to light and darkness. The germination of *B. quinata* seeds in light was significantly higher than in darkness at a range of constant temperatures from 20 °C to 35 °C. Dark germination was still considerably higher at optimal temperature (84 % at 20 °C), suggesting that light is not an absolute requirement for germination of *B. quinata* seeds, but its effect is temperature-dependent. *C. alliodora* also exhibited significant difference between light and dark germination for seeds incubated at alternating temperatures. Alternating temperature of low amplitude (5 °C) significantly enhanced germination in darkness (47 % in dark and 14 % in light at 20/15 °C). Baskin & Baskin (1998) point out that light requirement for germination may vary with temperature. Seeds of *L. divaricatum* and *T. rosea* germinated equally well in light and dark conditions; suggesting that germination in these species is not light-dependent (neutrally photoblastic).

Survival and growth

Survival of seedlings is greater in canopy gaps, compared with closed canopy, and is often higher in large gaps (Bullock 2000). It is evident from the present study that survival of transplanted seedlings over one year declined significantly under closed canopy compared with open sites. Poor survival under closed canopy is a direct consequence of low light intensity and perhaps poor spectral quality (red to far-red ratio). Faurby & Barahona (1998) pointed out that *T. rosea* is a pioneer species capable of establishing in small gaps in the forest, but its subsequent growth depends on availability of plenty of light. Brown & Whitmore (1992) stated that pioneer species respond only to major disturbances, not to small gaps, which partly explain why none of the planted seedlings of *T. rosea* survived in the partially-open site.

Shading has also been shown to increase seedling mortality indirectly by exacerbating fungal attack through increased humidity or by providing concealment for rodents, mollusks and land crabs that predate on seedlings (Augspurger 1984; Hanley *et al*. 1996; Sherman 2002). In addition, young seedlings also succumb to death due to physical damage induced by litterfall (Clark

& Clark 1991; Drake & Pratt 2001; Gillman *et al.* 2003; Mack 1998; Scariot 2000) under closed canopy than in large gaps. Our study showed that seedling survival also varied significantly among species. *C. alliodora* had the highest survival compared with *T. rosea* and *B. quinata*. Variation in seedling survival among species depends on the size and age of seedlings (Kitajima & Fenner 2000), and for dry forest species, a positive correlation between survival and initial seedling size has been documented (Gerhardt 1996). The large size of *C. alliodora* seedlings at the time of transplanting partly explains their high rate of survival compared with the other two species. Our finding is consistent with previous studies. For example, Guariguata (2000) reported a drastic decline in survival of transplanted *C. alliodora* seedlings under the forest canopy after one year, and Piotto *et al.* (2004) reported 73 % and 41 % survival for *C. alliodora* and *B. quinata*, respectively, after three years in pure plantations in Nicaragua. Gerhardt (1996) pointed out that high insolation during the dry season can lower survival significantly for some species by causing exacerbated desiccation of seedlings, which could be the case for *B. quinata* in our study which had the lowest survival among the studied species.

Subsequent growth of seedlings was favored in open than closed canopy, as evident from the significantly higher current annual increment in root collar diameter of *C. alliodora* seedlings in the present study. This could be related to reduction in competition for one or more resources in the open or partially-open sites, particularly light and soil moisture (Bullock 2000; Gerhardt 1996). In a study on another *Cordia* species (*C. africana*), Abebe (2003) has reported a significantly higher collar diameter increment for seedlings grown under full exposure to light than either 50 % or 25 % of the light intensity.

Conclusions

The optimal temperature for the germination of species tested in the present study appears to be between 20 °C and 30 °C. Light is not an absolute requirement for germination but its effect is modulated by alternating temperatures for some of the species. The result has an important implication for the restoration of abandoned fields. As seeds of the studied species germinate rapidly and to a larger extent, direct seeding of such pioneer species could be made. Seeds should be sown at a lower soil depth or should be covered with mulches

if sown at the surface to avoid desiccation, as diurnal temperature fluctuates much on open sites than under the forest canopy, and alternating temperature regimes tested in the present study tentatively proved inhibitory for germination. This does not necessarily mean that the temperature in the field fluctuates in a way similar to that under laboratory conditions. Further study to verify the effects of fluctuating temperature under field conditions is recommended. Survival of *C. alliodora* seedlings was considerably higher on open and partially-open sites with a significant increment in collar diameter while *T. rosea* had good survival on open site. This suggests that these two species could potentially serve as framework species for restoration of degraded and/or abandoned sites. Based on the current finding, *B. quinata* does not meet the requirement of framework species for restoring degraded sites in drier regions.

Acknowledgements

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