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Effect of leaf litter on seed dormancy, germination and seedling survival of three tropical forest tree species in Ghana

Hamza Issifu*, **Bernice A. Okyere, Rikiatu Husseini**

Department of Forestry & Forest Resources Management, University for Development Studies, Tamale, Ghana

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Abstract

The exact role of leaf litter and its interaction with irradiance in tree species regeneration is still poorly understood. We conducted a three – factor full factorial plant house experiment to determine the effect of leaf litter and irradiance (with particular interest in their interaction) on germination and seedling survival of three tropical tree species, namely; *Khaya anthotheca* (Welw.) C.DC., *Terminalia superba* Engl.& Diels and *Cedrela odorata* L. We made three predictions: 1. Seeds of tropical tree species take a longer period to germinate and also have lower germination percentage at full irradiance, 2. seedling survival is lower at full irradiance, 3. presence of litter at full irradiance reduces length of seed dormancy and increases seed germination and seedling survival. Our results indeed showed higher mean lengths of seed dormancy and lower germination percentages at full irradiance for all three species tested. Also, seedling survival was lowest at full irradiance and highest at intermediate irradiance. Germination percentages of all three species were higher with litter present than when litter was absent. The positive effect of litter on seed germination was higher at higher levels of irradiance. Presence of litter reduced length of seed dormancy only for seeds of *C. odorata*, but litter had no effect on seedling survival of any of the tested species, contrary to prediction. We suggest that very high irradiances may have adverse effects on regeneration of studied species, but presence of leaf litter may ameliorate adverse effects of high irradiance.

* **Corresponding Author:** Hamza Issifu ✉ hamza.issifu@gmail.com

Introduction

Forest tree species are known to vary in their requirements for seed germination (Vázquez-Yanes, 1974; Vázquez-Yanes & Smith, 1982; Kyereh *et al.,* 1999) and seedling establishment (Nunez-Farfan & Dirzo, 1988; Veenendaal *et al.*, 1996; Kyereh *et al.*, 1999). Based on these requirements, forest species have been classified into successional guilds; with pioneers regenerating only in open conditions and climax species regenerating mainly under forest shade (Swaine & Whitmore, 1988). While great differences exist between regeneration requirements of pioneers and non-pioneers, classification based on broad functional groupings could be concealing germination and survival responses of many forest species (Kyereh *et al.*, 1999). For example, species classified as pioneers remain dormant in the soil until a canopy opening occurs (Whitmore, 1975), but some other species classified as pioneers have been found to germinate in diffused irradiance under dense canopy shade (Kennedy & Swaine, 1992; Li *et al.*, 1996; Pearson *et al.*, 2002). Thus, differences in regeneration requirements among individual species appear more important than differences among guilds, and should still be investigated.

Open areas or large gaps in the forest are characterized by high irradiances and therefore, higher soil and air temperatures and higher evaporation rates beyond levels required for germination and establishment of many species (Chazdon and Fetcher, 1984; Pritchett and Fisher, 1987; Brown, 1994). Leaf litter tends to cover seeds in the forest floor (sometimes completely), which further regulates the conditions involved in the germination and establishment of seedlings (Molofsky and Augspurger, 1992), and in so doing may prevent germination and/or emergence particularly of small seeded pioneer species (Vazquez-Yanes & Orozco-Segovia, 1992; Dalling & Hubble, 2002).

Leaf litter may also have a positive effect on species establishment particularly at high irradiances, but this effect is not the same for all species (Molofsky and Augspurger, 1992). However, not many species have been tested for their germination and survival responses to this interaction effect of litter and irradiance. Therefore, this study was conducted with the following objectives:

1. to determine germination and survival responses of the three species to irradiance;
2. to determine the effect of leaf litter on seed germination and seedling survival;
3. to find out if germination and survival responses to irradiance of the three species are influenced by the presence of leaf litter.

We made three predictions as follows: 1. length of dormancy and germination percentage would be longer and lower respectively at full irradiance, 2. seedling survival would be lower at full irradiance, and 3. presence of litter at full irradiance would decrease length of seed dormancy and increase seed germination and seedling survival.

Materials and methods

Study site and species

The experiment was conducted at the plant house of the Nyankpala campus (latitude 09° 25′41"N and longitude 0° 58′42"W) of the University for Development Studies, Tamale, Ghana. The soil type in this area is mainly Alfisols with clayey loam and coarse-grave (CSIR-SARI 2008). Average high and average low temperatures for the month of May (when experiment was conducted) are 32°C and 27°C respectively, with slight yearly variations. Precipitation for the same period is usually around 110mm. (http://www.worldweatheronline.com/Nyankpala-weather-averages ass: 20/07/14; 14:00hrs).

Species used were *Terminalia superba* Engl. & Diels, *Cedrela odorata* L. and *Khaya anthotheca* (Welw.) C.DC., selected to represent a continuum of light requirement. *T. superba* is a pioneer species, *C. odorata* has intermediate light requirement while *K. anthotheca* is a shade bearer (Hawthorne, 1995; Poorter, 1999). Seeds of these species were collected from the high forest zone of Ghana by staff of the Seed Section of the Forestry Research Institute of

Ghana (FORIG) between November 2013 and February 2014 and stored in sealed plastic bags.

Experimental design and layout

The study approach was a manipulative plant house experiment. We employed a fully cross-factored, three factor design involving three species, three irradiance levels and two litter levels for this study. The three tree species have been described under "studied species" above. The three irradiance treatments were "no irradiance", achieved under a concrete slab in the plant house by covering the slab with an opaque plastic sheet; "intermediate irradiance", under a shed (with light thatch roof) adjacent the plant house; and "full irradiance", under full sunshine in the open areas outside of the plant house. Photosynthetically active radiation (PAR) was not measured, but irradiance categories were carefully selected to greatly vary irradiance amounts. The litter treatments were "litter present" versus "litter absent". Leaf litter (dead brown leaves) used for the experiment was collected from the moist semi-deciduous forest zone of Ghana where all three species used in this study occur.

In May 2014, 24 plastic buckets with dimensions 40 x 25 x 5cm were filled with top soil (savanna Alfisol soil type). Eight containers each were placed under the three irradiance levels. Ten seeds each of the three species were sown in each plastic container at a depth of 0.3 mm. Litter was placed on four containers at each irradiance level. The other four containers served as control (i.e. no litter). Litter thickness was 3 cm, made up of a pile of several leaves. This approach was different from that used by other authors, who used a litter layer of one leaf in depth placed directly on seeds (see Vazquez-Yanes & Orozco-Segovia, 1992). Our approach, which is similar to that used by Molofsky and Augspurger, 1992, was an attempt to simulate natural processes in the forest understory. Each plastic bucket received 1000 ml of water per day given in a twice-daily dose.

Data Collection and Analysis

We took weekly data on germination and survival for five weeks. At the end of the experiment, mean length of dormancy (i.e. how long it took for seedlings to emerge) was computed for all treatments.

Prior to data analysis, final germination and survival proportions were transformed using arcsine ($\sqrt{P}$), where "P" is germination or survival proportion, as suggested by Sokal and Rohlf (1995). Also, data on Mean Length of Dormancy (MLD) were ln-transformed to improve normality. We conducted a three-way ANOVA (or two-way ANOVA when species were analyzed separately) using general linear model (GLM) in SPSS, to compare mean germination proportion and mean length of dormancy (MLD) among treatments. The Tukey post-hoc test was used to compare means when a significant main effect of irradiance was found. Multiple comparisons when necessary were done with Sidak adjustment. A Kruskal-Wallis test was performed on seedling survival proportions as data failed to attain normality even after transformation.

Results

Effect of irradiance on seed dormancy and seed germination

There was a significant ($F_{(2, 67)} = 21.039$; $P < 0.001$) main effect of irradiance level on mean length of dormancy of studied species. Data for all species showed a general increase in length of dormancy with increasing irradiance level. However, multiple comparisons revealed significant differences in MLD among the three irradiance levels for seeds of two species (*K. anthotheca* and *C. odorata*) only (Fig. 1). We found a significant ($F_{(2, 72)} = 45.328$; $P < 0.001$) main effect of irradiance level on seed germination percent. Multiple comparisons showed mean germination percentages for all three species, to be lowest at full irradiance, differing significantly from both no-irradiance and intermediate irradiance treatments (Table 1).

Effect of irradiance on post-germination seedling survival

For all species data analysed together, seedling survival followed a similar pattern as seed germination. Results of a Kruskal-Wallis test performed on survival proportions indicate significant (Chi-Square = 17.342, d.f. = 2, $P < 0.001$) differences among the three irradiance levels. Survival was highest at intermediate irradiance levels (with 24.3%), differing significantly from both no-irradiance and full-irradiance levels, which recorded 10.9% and 4.2% respectively. No significant differences existed between survival at full-irradiance and no-irradiance treatments (Fig.1).

Table 1 Estimated marginal means of germination percentages under contrasting irradiance levels. Superscript letters compare means (within species only). Significant differences at alpha level of 0.05 are shown with different letters in superscript.

Irradiance level	Germination percentage		
	K. anthotheca	T. superba	C. odorata
Full-irradiance	15.00^{b}	17.50^{b}	25.00^{b}
Intermediate-irradiance	50.00^{a}	35.00^{a}	58.75^{a}
No-irradiance	63.75^{a}	36.250^{a}	67.50^{a}

When species were analyzed separately, this general pattern of survival was shown in *K. anthotheca* and *C. odorata*. Although, a similar survival pattern existed among seedlings of *T. superba*, no significant differences were found among the three irradiance treatments (Table 2).

Table 2. Mean survival proportions of species at the three irradiance levels. Attached letters (in superscript) compare means (within species only). Different letters indicate significant differences at alpha level of 0.05).

Irradiance level	Seedling Survival proportion		
	K. anthotheca	T. superba	C. odorata
Full-irradiance	0.0873^{a}	0.190^{a}	0.000^{a}
Intermediate-irradiance	0.5102^{b}	0.407^{a}	0.443^{b}
No-irradiance	0.4195^{a}	0.015^{a}	0.149^{a}

Effect of litter and its interaction with irradiance on seed dormancy, seed germination seedling survival

For all species data analyzed together, litter was found to have significantly increased germination percentage, with a higher mean germination percent of 48.6 on litter-present plots compared with mean germination percent of 33.3 on control (litter-absent) plots. Multiple comparisons of litter effects at the three irradiance levels revealed the following; at no-irradiance, litter had no significant ($P = 0.328$) effect on seed germination, but at intermediate-irradiance, there was a significant ($P = 0.001$) effect of litter on seed germination, while this effect was found at an even higher level of significance ($P < 0.001$) at full-irradiance level. However, the effect of litter on MLD and seedling survival was not found to be significant (Fig. 4).

When species were analyzed separately, presence of litter significantly increased germination percent of *K. anthotheca* seeds only at full irradiance (Fig3). For this species, litter did not significantly affect MLD or seedling survival (Figs. 4 and 2 respectively), although the few remaining seedlings at the end of the experiment were all found on litter-present plots.

Germination response of *T. superba* seeds to litter was significant only at full irradiance (Fig. 3). At this level of irradiance, seed germination was higher in litter-present plots than in the litter-absent plots. However, MLD and seedling survival of *T. superba* were not significantly affected by litter treatments (Fig. 4).

In seeds of *C. odorata*, litter application significantly increased seed germination at all irradiance levels (Fig. 3). MLD was also found to be significantly longer in the absence of litter than in litter-present plots. This effect was particularly stronger at full irradiance (Fig. 4). *C. odorata* seedlings did not survive at full irradiance regardless of litter treatment, and no significant effect of litter was found at either intermediate or no-irradiance levels (Fig. 2).

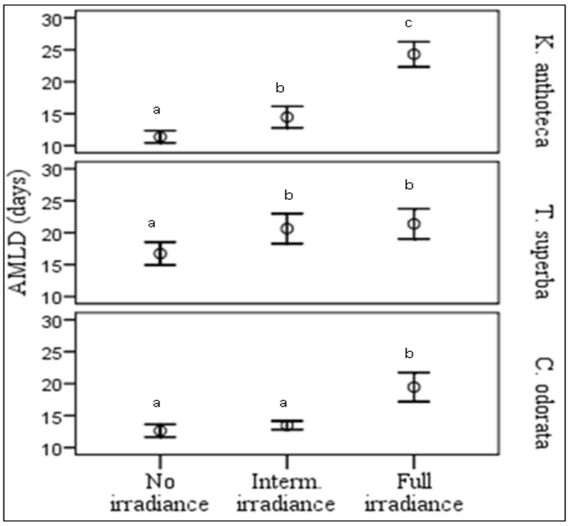

Fig. 1. Mean length of seed dormancy (AMLD) of the tested species under different irradiance levels. Error bars represent +/-1 SE of mean. Letters used for comparisons (within species only). Different letters indicate significant differences at 0.05 alpha level.

Discussion

Effect of irradiance on length of seed dormancy, seed germination and seedling survival

We predicted that period of seed dormancy would be longer at full irradiance, culminating in lower seed germination. Our data revealed that for all three species tested (regardless of the successional guild to which they belong), the lowest germination percentages were recorded at full irradiance. Also, period of seed dormancy was relatively longer at full irradiance for seeds of two species (*C. odorata* and *K. anthotheca*). This finding lends credence to our prediction and also confirms findings of Kyereh *et al.* (1999), who reported that both germination percentage and speed of germination of many tropical forest tree species were adversely affected by high irradiance. Very high irradiances are very often confounded by many other adverse environmental factors such as high soil and air temperatures (Chazdon and Fetcher, 1984; Pritchett and Fisher, 1987; Brown, 1994) as well as rapid evaporation rates (Chazdon and Fetcher, 1984; Fetcher *et al.*, 1985) on the forest floor. These factors possibly explain the adverse effect of full irradiance on the studied species.

We also predicted that post-germination seedling survival would be lower at full irradiance. We found this to be the general pattern of survival, but when species were analysed separately, we found this effect for two species (*C. odorata and K. anthotheca*). Whereas *K. anthotheca* is a shade bearer, *C. odorata* has intermediate light requirement, therefore seedlings of the two species suffered the highest mortality under full irradiance while those of *T. superba* (a typical pioneer) remained relatively unaffected. Thus, successional guild to which species belong apparently determined post-germination seedling survival. However, we suggest that higher temperatures and higher evapo-transpiration rates known to characterize higher irradiances may have played a more important role in determining observed seedling survival responses at full irradiance.

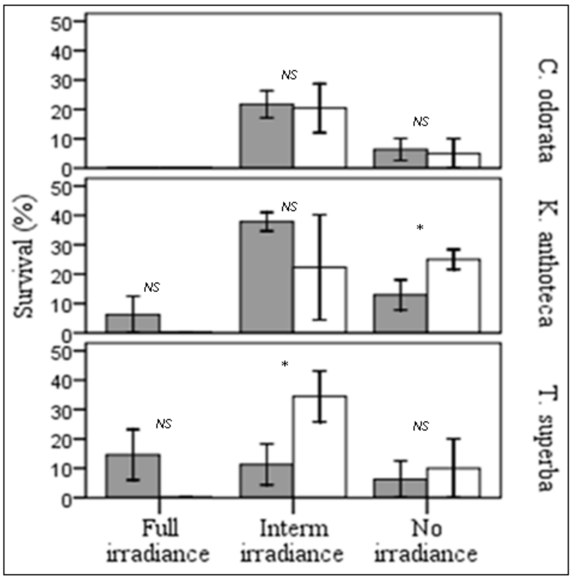

Fig. 2. Percentage survival of seedlings in litter (filled bars) and no-litter (open bars) treatments at different irradiance levels. Error bars represent +/- 1 SE of mean. Significant differences indicated by asterisks. *NS* indicates no significant difference (at 0.05 alpha level). Comparisons within species only.

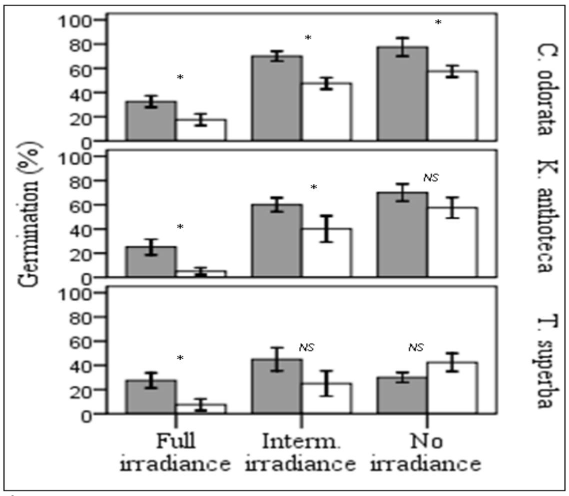

Fig. 3. Germination percentage of species in litter (filled bars) and in no-litter (open bars) treatments at different irradiance levels. Error bars represent +/- 1 SE of mean. Significant differences indicated by asterisks. *NS* indicates no significant differences (at 0.05 alpha level). Comparisons within species only.

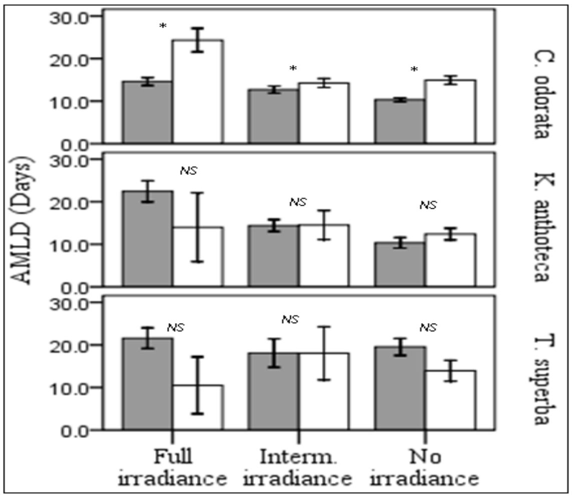

Fig. 4. Mean length of dormancy (AMLD) of species in litter (filled bars) and in no-litter (open bars) treatments at different irradiance levels. Error bars represent +/- 1 SE of mean. Significant differences indicated by asterisks. *NS* indicates no significant difference (at 0.05 alpha level). Comparisons within species only.

Effect of litter and its interaction with irradiance on dormancy, germination and seedling survival

We predicted that presence of litter at full irradiance would reduce period of seed dormancy and increases germination and post-germination seedling survival of tested species. Indeed, higher germination percentages were recorded in the presence of litter than in its absence for all tested species. This effect of litter was regardless of successional guild to which the species belong, but we did not find any effect of litter on seed dormancy or on seedling survival. These findings were partly consistent with our prediction, but contradict the many studies that suggest a negative effect of litter on seed germination and seedling emergence of certain tropical tree species (Thompson *et al.*, 1977; Campbell *et al.*, 1989 Vazquez-Yanes *et al.*, 1990; Vazquez-Yanes & Orozco-Segovia, 1992; Molofsky and Augspurger, 1992) particularly, of small-seeded pioneers. Some authors (e.g. Molofsky and Augspurger, 1992) have reported adverse effects of litter only under very thick litter layers. Reason for this finding could be that under low irradiance an additional layer of litter covering seeds already buried in the soil will create excessive darkness, greatly altering light quality reaching small seeds. However, Molofsky and Augspurger (1992) also found that some large-seeded species established better under litter in full irradiance, and that deeper layers of litter were necessary for establishment of some seedlings under high irradiance. Species in our study were chosen to represent a continuum of light requirement, but all species responded similarly to litter. However, like Molofsky and Augspurger (1992), we also found that litter was more important for seed germination at higher irradiances. These findings imply that some of the adverse microclimatic factors that characterize very high irradiances were ameliorated by presence of litter, suggesting that litter plays a positive role in seed germination of some species perhaps, by providing conditions similar to those provided by canopy cover.

Findings in this study have the implication that regeneration of some tropical forest species (regardless of the successional guild to which they belong) will be greatly hampered by the creation of very large gaps which allow maximum irradiance to hit the forest floor. Our findings also suggest that presence of leaf litter at high irradiances has a positive role in species establishment. However, because we did not experiment with various litter thickness, we propose further experiments with different litter levels and different species, as the exact effects of litter and its interaction with irradiance on species establishment appear dependent on species type, but hardly on broad functional groupings.

Conclusion

Exact effect of the interaction of leaf litter with irradiance on regeneration of tropical tree species has been a long standing question in ecology. It is recognized that important differences exist among species within successional guilds. For all three species tested in this study, length of seed dormancy is longer at full irradiance. Seed germination percentage is also lower at full irradiance. Initial seedling survival (following germination) generally tends to be highest at intermediate level of irradiance and lowest at full irradiance for all three species.

Our data also reveal relatively higher germination percentages with presence of litter at full irradiance for all tested species. Presence of litter reduces length of dormancy for only *C. odorata* seeds. At full irradiance leaf litter did not (statistically) affect seedling survival in this study, contrary to prediction. This we attribute to the very low seedling survivorship at full irradiance. Nonetheless, the few surviving seedlings at the end of the experiment were all found in litter-present plots. Thus, litter appears important for survival of seedlings at high irradiances.

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