Uganda Journal of Agricultural Sciences, 2002, 7: 25-30
Printed in Uganda.

ISSN 1026-0919

Influence of light quality on the germination characteristics of seeds of selected pioneer, understorey and canopy tree species in Kalinzu forest reserve, Uganda

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Abstract

The effect of light quality and sowing depth on seed germination of selected pioneer, understorey, secondary colonizer and canopy tree species in Kalinzu Forest Reserve was studied. Seeds of different species were sown under incident radiation, neutral shade, interrupted leaf shade, continuous leaf shade, different coloured lights, darkness, on the soil surface and in the soil at a depth of about 1.5 cm. There were interspecific variations in percentage, rates and periods before initiation of germination among the different light treatments. Seeds of the selected pioneer species (*Musanga leo-arrerae* Hauman & Leon) only germinated under incident light, neutral shade, interrupted leaf shade, red light and on the soil surface. Ninety seven percent of the seeds germinated under incident light and 4% under interrupted leaf shade. Seeds of *Albizia gummifera* J.F. Gmel (secondary colonizer), *Oxyansus speciosus* DC (understorey) and *Funtumia africana* Benth. (canopy) germinated under incident radiation, neutral shade, interrupted leaf shade, continuous leaf shade and darkness. Seeds of the pioneer species germinated only on the soil surface because of the steep light gradient in the upper soil layers. Seeds of the sub-canopy species germinated both below (with a higher percentage) and on the soil surface.

Key words: Seed germination, light, pioneer, understorey, canopy

Introduction

Light quality and intensity are some of the factors, which influence germination of tree seeds (Fenner, 1980; Drake, 1993). According to Hart (1988), seeds can be classified as positively photoblastic, negatively photoblastic and light neutral. Light quality, rather than light intensity, may affect seed germination (Vasquez-Yanes & Orozco-Segovia, 1993). Previous studies have shown that a phytochrome is associated with the mechanisms that control seed germination responses to light (Orozco-Segovia & Vasquez-Yanes, 1989). Therefore, in a typical photochrome mediated response, germination is usually promoted by light with a high red/far ratio and inhibited by light with a low red/far-red ratio usually found beneath the vegetation canopy (Drake, 1993).

Under the vegetation canopy, the photon flux density is often greatly reduced through absorption by photosynthetic pigments and the red/far-red ratio is altered (Hart, 1988). Under a tropical forest canopy, the red/far-red ratio range may be as low as 0.22 –0.77 compared to direct light where the ratio is about 1.2 (Hart, 1988). Light is also strongly attenuated by soil, although seeds located in the deeper soil layers are in perpetual darkness (Thijs, 1993). A 5.0 mm depth below the soil can have a red/far-red ratio of 0.5 –0.8 and the ratio varies with the type of soil (Hart, 1988). As a result, there are often variations in germination responses among plant species because of the steep light gradient in the upper soil layers (Bliss & Smith, 1985). According to Thijs (1993), light can stimulate and/ or inhibit seed germination even in a few millimeters of soil.

Tropical forest trees have been categorized on the basis of their light requirements for germination. According Everham *et al.* (1996), germination of seeds of pioneer tree species is enhanced by direct solar radiation. On the other hand, Ellison *et al.* (1993) noted that seeds of the understorey species usually germinate under different micro-environmental conditions. In reference to the spectral composition of light, Metcalfe (1996) noted that tropical rain forest species that colonize open and disturbed habitats often demand red light for germination and are inhibited by wavelengths in the far-red region. Clark & Clark (1987) also noted that many tree species fall between these two limits (pioneer and shade tolerant) thus combining rapid germination and shade tolerance following increased light availability due to canopy opening. The inability of light inhibited seed to germinate near the soil surface can influence its survival during dry conditions. At the same time, the demand for direct light for germination enables seeds to germinate under less competitive situations (Fenner, 1980).

Seed germination is one of the key plant processes affected by forest disturbances because of microhabitat conditions such as light and temperature are altered (Denslow, 1987). For a given seed population, percentage germination reflects a natural variation in response to certain environmental factors (Hart, 1988).

Kalinzu Forest Reserve has experienced human disturbances in the past (Forest Department, 1996) and the light regime in several areas have been modified and the forest soil disturbed. Since light is of great ecological significance in forest regeneration, the study was carried out with the aim of establishing the germination rates and percentages of seeds of various tree species under different light qualities. This information does not exist for Kalinzu and other natural forest reserves in Uganda. The hypotheses tested was that varying light qualities and depth of sowing influences germination of seeds of different tree species. The data presented here would therefore help in the planning and management of tropical forest reserves and development of management interventions to enhance forest productivity and ecological balance.

Materials and methods

Study site

Kalinzu Forest Reserve is a tropical rain forest located in south-western Uganda between 0°17' 50" 30' S and 30° 00' 30° 07'E. It has an area of 137 km² and lies between 1250-1827 m above sea level on the eastern slopes and upper edges of the western rift valley. The forest comprises a wide variety of forest types broadly classified as medium altitude moist evergreen and semi-deciduous forest (Howard, 1991). The forest has 265 tree species (57% of the country's total) and is dominated *by Parinari excelsa, Carapa gradifolia, Strombosia scheffleri, Funtumia africana, Musanga leo-errerae* and *Taberbaemontana holstii.*

The study was undertaken in three forest types: mechanically logged, heavily pitsawn, and relatively pristine. The tree species studied were *Musanga leo-errerae* Hauman & Leon (a pioneer species), ***Albizia gummifera*** J.F. Gmel (a secondary colonizer), ***Oxyansus speciosus*** DC (an understorey species), *Funtumia africana* Benth. (a sub canopy species), *Strombosia scheffleri* Hook., ***Parinari excelsa*** Engl. and *Trema orientalis* Ficalho.

Effect of simulated forest light conditions on seed germination

Two sets of 50 seeds from the tree species mentioned above were exposed to incident light to simulate a big forest gap. A second set of 50 seeds was covered with green banana leaves to simulate the forest understorey microenvironment (Fenner, 1980). The banana leaf petioles were put in a basin of water to keep them fresh and were replaced after every two days. The third set of 50 seeds were also covered with green banana leaves but the leaf shade was removed for one hour after every two hours. This simulated a forest canopy with small openings through which direct light reaches the forest floor periodically. This has been referred to as interrupted leaf shade (Fenner, 1980). A fourth set of 50 seeds were covered with white paper known to transmit nearly equal amounts of red and far-red lights (Fenner, 1980). A fifth set of 50 seeds were kept in the dark by covering them with a perforated black polythene sheet which permitted aeration in the box. Seed germination was monitored and recorded over a period of 30 days. In each petri dish (10 cm in diameter), the seeds were placed on two layers of filter paper saturated with distilled water (Fenner, 1980).

Effect of colored lights on seed germination

Fifty seeds each of *M. leo-errerae, O. speciosus, F. africana* and *F. gummifera* were placed on a 10 cm diameter petri dish having two layers of filter paper saturated with distilled water (Fenner, 1980). Two replicates of seeds of each species were placed in white painted boxes (Synnot, 1975). Each box had apertures at the top and the side to allow insertion of the petri dishes and inspection of the seeds. The boxes were left uncovered, covered with red, blue and green lights and a black polythene sheet. The seeds were then examined for germination for 30 days.

Effect of depth of sowing on seed germination. The hypothesis tested was that, the depth at which the seeds are buried in the soil affects germination of seeds of different tree species. Two replicates each containing 50 seeds of *M. leo-errerae, T. orientalis* (pioneer species), *F. africana, S. scheffleri* and *P. excelsa* (canopy species) were sown on the soil surface and below the soil surface at a depth of about 1.5 cm and monitored for four months. On the dry days, the seeds were watered in the morning and evening to maintain adequate soil moisture needed for germination.

Results

Effect of simulated forest light conditions on seed germination

There were interspecific variations in the germination percentages among the different light treatments. For instance, seeds of *F. africana* (sub-canopy species), *O. speciosus* (understorey species) and *A. gummifera* (secondary colonizer) germinated in all the five light treatments. Seeds of *O. speciosus* (understorey species) had the lowest percentage germination in all the treatments (Table 1). The seeds of *M. leo-errerae* (pioneer species) did not germinate in darkness, had the lowest germination percentage under leaf shade (< 5%) and the highest germination percentage under incident light. A chi-square test showed that there was a significant difference in the germination percentage of seeds of the selected tree species under different light treatments (X^2=67.47, DF=8 and P<0.001).

With the exception of seeds of *M. leo-errerae* that had the highest percentage germination under incident radiation, all the other seeds had the highest germination percentages under neutral shade. Moreover, the germination percentage of the *M. leo-errerae* seeds sown under incident light (97%) was not significantly greater than those under neutral shade (86%) (Wilcoxon signed rank test: T=22.5, n=12, P>0.05).

It was further found that the seeds of *A. gummifera* had a high germination percentage in every light treatment (mean range of 80% to 90%) whilst the seeds of *O. speciosus* had the lowest percentage germination (mean range of 4%-46%). The differences in the germination percentages of *A. gummifera* seeds exposed to the different light treatments were not significant (X^2=3.91, DF=4, P>0.05) while those of *O. speciosus* were significant (X^2=46.1, DF=4, P<0.0).

There were significant differences (X^2=13.06, DF=3, P<0.01) in the time taken to initiation of germination of seeds of the four species under the different light treatments (Table 2). For example, seeds of *A. gummifera* took the shortest time (2 days) to germinate whilst seeds of *O. speciosus* exposed to incident radiation took the longest time (25 days). For each of the species, time to initiation of germination was the same or nearly equal among the different treatments. This trend did not however apply to *O. speciosus* seeds under all the treatments.

Rates of germination varied among the species and the different light treatments (Figure1). *Albiza gummifera* seeds followed by *M. leo-errerae* had faster rates of germination than the other species. More than 50% of the seeds of *A. gummifera* and *M. leo-errerae* germinated within 12 days in the light treatments where each was able to germinate (Figure 1). On the other hand, seeds of *O.speciosus* had the slowest germination rate because less than 50% of the seeds in any light treatment had germinated by the 30th day of sowing. There were no significant differences (X^2=1.85, DF=4, P>0.05) in the rates of germination of seeds of *A. gummifera* and *F. africana*, that had at least 50% of their seeds germinating in three treatments within the 30 days.

Each species had its pattern of germination rates under the different light treatments. For example, *M.leo-errerae* seeds exposed to incident light consistently germinated faster than those exposed to neutral shade. *Oxyansus*

Table 1. Percentage seed germination of four tree species under five light treatments for 30 days

Species	Incident light	Neutral shade	Interrupted leaf shade	Continuous leaf shade	Darkness
Musanga leo-errerae	97(6)	86(7)	4(1)	0.5	0
Albizia gummifera	86(3)	92(2)	90(4)	80(2)	84(1)
Oxyansus speciosus	4(1)	46(9)	12(4)	28(3)	7(2)
Funtumia africana	56(6)	88(4)	80(3)	76(2)	20(3)

Figures in brackets are the ranges of the two replicates.

Table 2. Time (days) taken for initiation of germination of seeds of four species exposed to different light treatments

	Period taken for germination to occur				
Species	Incident	Neutral light	Interrupted shade	Continuous leaf shade	Darkness leaf shade
Musanga leo-errerae	6	7	7	8	0
Albizia gummifera	3	3	2	3	2
Oxyansus speciosus	25	9	16	19	8
Funtumia africana	10	11	9	10	18

speciosus seeds had the fastest germination rate under neutral shade and slowest rate under incident light. Germination rates of seeds of *F. africana* and *A. gummifera* exposed to darkness and continuous leaf shade were slower than in the other treatments.

The time taken for all the viable seeds to stop germinating also varied among the species and light treatments (Figure 1). Seed germination stopped earliest (on the 11th day of sowing) among *A. gummifera* seeds and latest among *O. speciosus* seeds (Figure1). The seeds of *O. speciosus* sawn and exposed to interrupted and continuous leaf shades were still germinating by the 30th day and no more germination occurred thereafter.

Effect of colored lights on seed germination

Musanga leo-errerae seeds germinated under incident and red coloured lights only (Figure 2) while *A. gummifera* seeds germinated under incident light, darkness and in red and green colored lights (Figure 3). For both species, the seeds exposed to red light had higher germination percentages (*M. leo-errerae* 94% and *A. gummifera* 86%) than those exposed to the other treatments.

Germination of *M. leo-errerae* seeds started after eight days and by the 24th day, it ceased in both types of light treatments. The rate of germination of seeds exposed to red light was consistently higher than those exposed to the other light treatments (Figure 3).

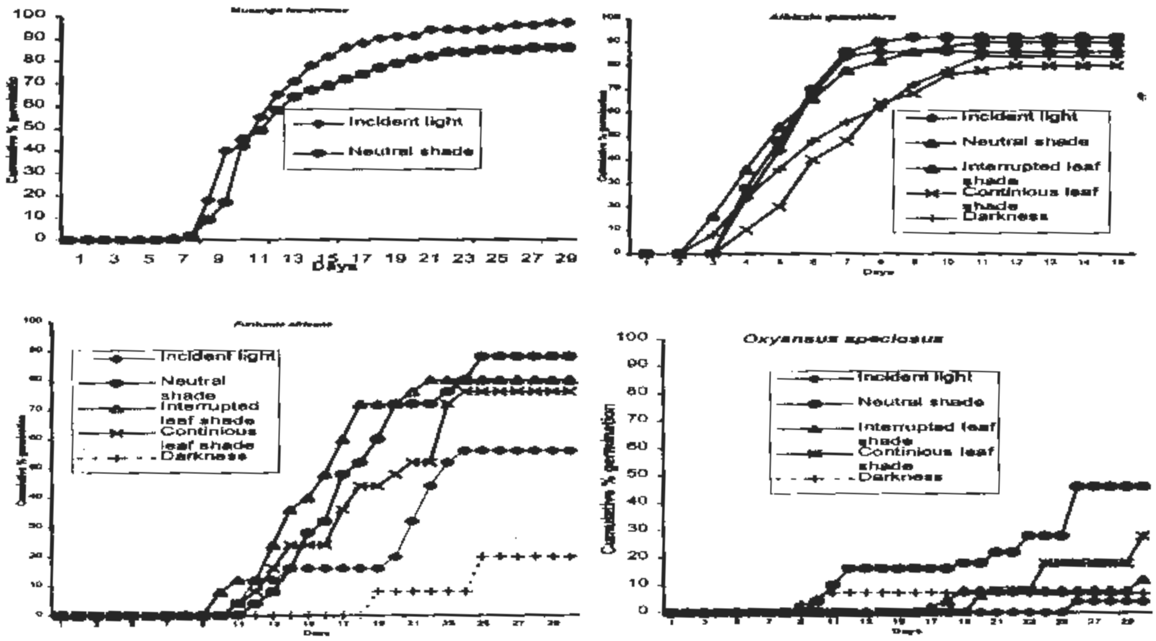

Figure 1.Cumulative percentage germination of seeds selected species exposed to different different light treatments

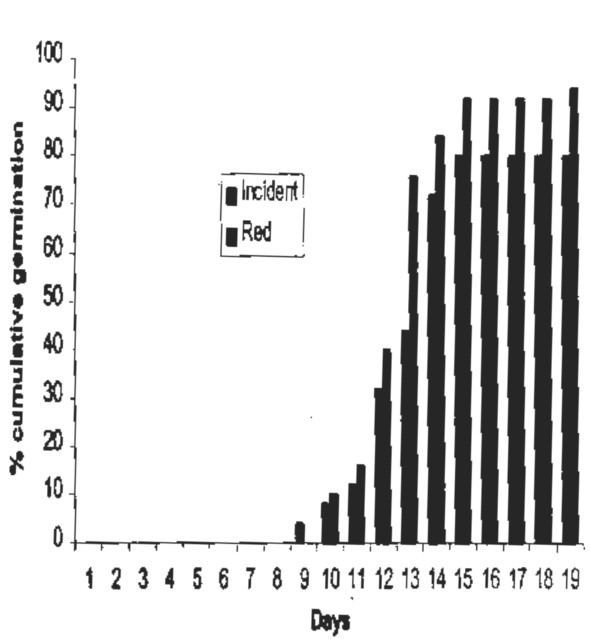

Figure 2. Cumulative percentage germination of *Musanga* leo-errerae seeds exposed to incident and red lights.

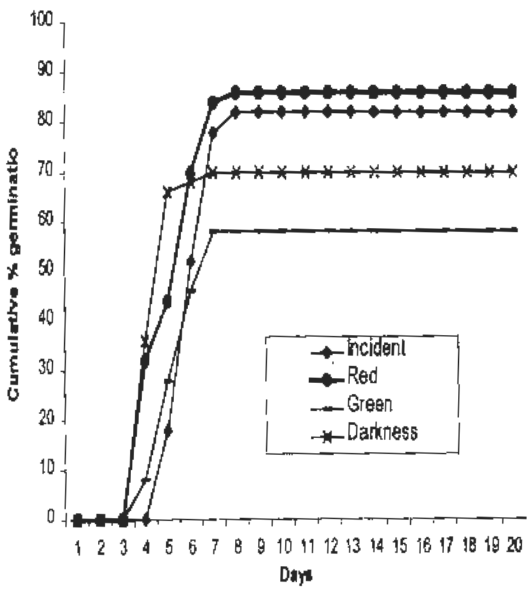

Figure 3. Cumulative percentage germination of ***Albizia gummifera*** seeds exposed to different light treatments.

Germination of *A. gummifera* seeds was initiated three days after sowing (Figure 3) and stopped within eight days. *Albizia gummifera* seeds exposed to red light germinated faster (86% had germinated after nine days of sowing) than those exposed to other light treatments. Seven *A. gummifera* seeds exposed to green light decayed while all the seeds exposed to blue light were infected by fungus and decayed.

Less than 20% of the seeds sown on the soil surface germinated and about 10% of the seeds sown in the soil germinated (Table 3). *Musanga leo-errarae* and *Trema orientalis* seeds sown below the soil surface did not germinate. Seeds of *F. africana* and *S. scheffleri* germinated in both soil locations. A higher proportion of seeds of *F. africana* (68%) and *S. scheffleri* (52%) germinated in the soil than on the soil surface (Table 3). Eighty four percent of *S. scheffleri* seeds germinated in the soil and 44% on the soil surface; only one *Parinari excelsa* seed was able to germinate.

Table 3. Cumulative percentage germination of seeds of selected tree species sown at and below the soil surface.

Species	Seed location	
	On the soil surface	Below the soil surface
Musanga leo-errarae	38.0(+6)	0
Trema orientalis	20.0(+4)	0
Funtumia africana	52.0(+7)	68.0(+6)
Strombosia scheffleri	44.0(+2)	84.0(+8)
Parinari excelsa	0	2.0

* values in parentheses are ranges of germination percentages between the replicates.

Discussion and conclusions

The variations in germination percentages of seeds of the forest tree species demonstrated that they respond differently to various light qualities with respect to succession stages of tropical plants. For example, it has bee found that while seed germination of the secondary colonizer (*A. gummifera*), understorey (*O. speciosus*) and sub-canopy (*F. africana*) species can occur in lights of diverse spectral composition, that of the pioneer species (*M. leo-errerrae*) is restricted to either incident, red or neutral shade. This observation concurs with the findings of Everham *et al.* (1996) and Metcalfe (1996) who reported that the seeds of most pioneer tree species only germinate in gaps where they are exposed to direct solar radiation while seeds of other succession stages germinate in diverse light environments.

The failure of seeds of the pioneer species to germinate in darkness while they germinated in other light treatments shows that darkness inhibits their seed germination. Since the germination of seeds of *M. leo-errerae* was induced by incident radiation and yet inhibited by darkness, they can be referred to as being photoblastic (Orozco-Segovia *et al.*, 1993).

The germination of some seeds of *M. leo-errerae* under interrupted leaf shade suggests that a brief exposure to incident radiation stimulates germination. However, since the germination percentage was very low compared to that under red and incident light or neutral shade, it can be concluded that *M. leo-errerae* seeds need exposure (>2hours) to incident radiation in order to germinate. This finding agrees with those by Orozco-Segovia *et al.* (1993) who noted that the germination of photoblastic seeds under closed canopy in tropical rain forests increases with the frequency and duration of sunflecks in the forest.

Very low germination under continuous leaf shade (0.5%) and the failure to germinate in green and blue coloured lights suggest that leaf shade and other lights in the far-red region also inhibit seed germination. Similar observations were also reported by Hart (1988) that germination of seeds of light demanding tree species is inhibited by light with low re/far-red ratio as is the case with continuous leaf shade, green and blue coloured lights commonly found on the floor of a dense forest.

As reported by Ellison *et al.* (1993), the ability of seeds of the secondary colonizer, understorey and sub canopy tree species to germinate in the diverse light conditions suggest that the quality of light is not a basic factor for seed germination. Metcalfe (1996) also noted that seeds of understorey tree species germinate under different micro-environmental conditions such as in the green shade or in darkness. The ecological significance of this observation is that these species can successfully regenerate under different forest conditions. For example, since *Albizia gummifera* is a secondary colonizer commonly found in cleared forest areas, the ability of its seeds to germinate under different light qualities and in darkness is a feature that enables it to regenerate even under dense ground vegetation cover. Unlike seeds of the non-pioneer species, the seeds of *Funtumia africana* (canopy tree species) had relatively low percentage germination in darkness thus indicating that darkness hinders the germination.

Several conclusions can therefore be drawn from this study. Firstly, the time taken for sown seeds to commence germination and the rate of germination in general varied among the tree species and light conditions in the forest. Though environmental factors such as light are expected to be associated with this, the basic cause for the variation is possibly genetic in nature. For example, the faster rate of germination of *F. africana* seeds under incident light than in the other light treatments implied that light with higher Red:Far-red ratio enhances the germination of seeds of this species compared to light with equal or high Far-red:Red ratios. As Metcalfe (1996) suggested, it can also be generalized that faster germination of seeds in the green shade than in the dark suggests that these species might be responsive to the wavelengths passing through the green canopy in the forest.

Secondly, the relatively large differences in germination rates of the seeds of *O. speciosus* in different light treatments could have possibly been due to certain inherent characteristics that influence their responses to varying environmental conditions. Past studies have shown that some seeds can differ in their sensitivity to light (Ellis *et* *al.*, 1989; Orozco-Segovia *et al.*, 1993) and the sensitivity varies among seeds of the same cohort due to differences in the concentrations of photochromes (Orozco-Segovia & Vasquez-Yanes, 1989).

Thirdly, the secondary colonizer (*A. gummifera*) has a very high rate of seed germination. It has become clear that the imbibed seeds of *A. gummifera* were susceptible to pathogenic infections, which caused them to rot. The rapid germination rate can therefore be an ecological advantage since emerged seedlings can escape some of these mortality factors. Furthermore, the relatively high germination rate of the small-seeded pioneer species such as *M. leo-errerae* enables it to take advantage of open forest conditions such as a gap before it is invaded by ground vegetation cover or is covered with litter.

Fourthly, the ability of *M. leo-errerae* and *T. arientalis* seeds to germinate on and not below the soil surface can be attributed to the photoblastic nature of these pioneer tree species. According to Hart (1988), positively photoblastic seeds do not germinate below the soil even at a depth of 1.0 mm because of the law Red:Far-red ratio (<0.5). Although *M. leo-errerae* and *T. orientalis* are pioneer species, differences in percentage germination of their seeds are not unique because of their genetic differences. Studies on seed germination by Vasquez-Yanes & Orozco-Segovia (1996) have shown that photoblastic seeds of different species differ greatly in their responses to Red:Far-red ratios due to variations in levels of phytochromes. The data presented here indicate that the germination of *M. leo-errerae* seeds is more stimulated by incident radiation than those of *T. orientalis*. However, because of the small number of seeds that germinated, it is not possible to generalize the responses of the seeds of these species to direct solar radiation.

Germination of seeds of both sub-canopy species (*S. scheffleri* and *F. africana*) on and below the soil surface suggests that light may not be a key factor limiting the germination and because the light requirements for seed germination of both species are similar. The obvious reason is that both species are sub-canopy and shade tolerant trees growing in similar environmental conditions in the forest. But since these species had higher percentage germination below than on the soil surface, it can be concluded that darkness favoured their germination or other factors not examined in this study could have been involved.

Acknowledgements

The research leading to this article was undertaken as part of the first author's Ph.D. study funded by the Government of Norway through Makerere University-NUFU Programme. We thank the African Academy of Sciences for supporting the fieldwork. Many thanks to the field assistants who helped with data collection. We also thank the two anonymous reviewers for their valuable comments on the earlier version of the manuscript.

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